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THE BURROWING OWL, ITS BIOLOGY AND MANAGEMENT

INCLUDING THE PROCEEDINGS OF THE

FIRST INTERNATIONAL BURROWING OWL SYMPOSIUM

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Daniel E. Varland
Special Publications Editor

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DEDICATION

This Raptor Research Report, which focuses its attention on the burrowing owl, is dedicated to Dick and Joan Clark for their tireless and selfless raptor conservation, research, and educational efforts. To them, as our colleagues and friends, we gratefully take this opportunity to say 'thank you'.

J. Raptor Res. Report 9:1

FOREWORD

Although I was never sure that I was the most appropriate person to preface this symposium volume, having been chosen (and therefore sufficiently flattered), it is with great satisfaction that I wish to put in print my impressions about the importance of the work commented henceforth.

This volume is a step forward in providing not only information on burrowing owl biology, but also on its practitioners. Bird-watchers, college and graduate students, academics and professionals will find in a nutshell what has been published in the past about this owl, what is the state of the art, and the addresses of people to contact for further information. This data-filled monograph should be of much utility to anybody wishing to join the ranks of burrowing owl students, and to fellow raptor biologists to learn from and reach out to their previously unknown colleagues in different states and countries.

The subject of the enormous accumulation of knowledge reported in this book is a unique species in several respects. The burrowing owl has a peculiar aspect, biology and distribution. This long-legged creature is generally diurnal, easy to spot due to its preferred open habitats, nests on the ground, and is distributed from Canada to the tip of South America.

The first two features of this owl, diurnality (which is unusual among owls) and use of open habitats, contribute to the enjoyment of amateur bird-watchers, and render it an ideal subject for study by raptor biologists. On the other hand, the third feature mentioned, its nesting on the ground (in the same open and flat areas favored by us humans to develop agriculture and to establish our urban developments), frequently places us in conflict with the burrowing owl. We have the same habitat requirements, and apparently are winning our competitive contest, in both exploitative and interference ways.

Although the burrowing owl is extensively distributed in the Americas, so are we. Cornered, and with no place left to escape, it seems a moral imperative that we humans take care of this little companion during our travel in Spaceship Earth. If this owl cannot renounce to the ecological traits that thousands of years ago made it perfectly fit to live as it chose, then we will have to give up claiming some of its land or otherwise compensate it somehow.

The search for such a compromise demands the concurrence of experts from many fields: anatomy, behavior, conservation, ecology, environmental education, physiology, genetics, reproduction, taxonomy, systematics, wildlife management, etc. It also requires input from many professionals: biologists, veterinarians, rehabilitators, land managers, urban developers, and, indeed, individuals from all walks of life, from students of all grades, to park rangers, politicians, and citizens in general.

Too much to ask? Apparently not. Judging from the variety of contributors to this volume, I see a broad cross-section of disciplines and professionals aiming at understanding the threats and necessities of the burrowing owl and providing some solutions. As long as this situation remains, and more people are incorporated into appreciating the desirability of coexisting with our fellow neighbor, the burrowing owl, there is hope that we may reach a compromise.

There is a final aspect that may facilitate a convergence of wills toward putting up the burrowing owl as an honorable case of meeting our respective demands in the middle. In the same way as the cosmopolitan barn owl may be considered as a raptorial world ambassador, the burrowing owl is an ambassador for the Americas (all three of them, and the Caribbean). They share some behavioral traits with our human ambassadors: they tend to live under the spotlight, travel a lot, and are located in many American nations. Sometimes they are threatened, and, like the burrowing owl, require strong backing from their governments.

The constituency of our ambassador, the burrowing owl, is us—the human beings. I believe that it is in the best of all our interests to provide comfort and support to our owl. I see in this volume that I am prefacing that we are off to a good start. Let's make it to the finish line!

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BACKGROUND

Origins. The conception of the First International Burrowing Owl Symposium (BOS) can be traced back to conversations with Paul James and Joe Schmutz. Each expressed concern over the fate of the burrowing owl (*Speotyto cunicularia*) in their country, Canada, and throughout its range.

Embryonic development of this effort followed discussions with Butch Olendorff, Dick Clark, and Jack Barclay, which confirmed the level of concern and the identification of our BOS Steering Committee. The Steering Committee was made up of eleven individuals from the United States, five from Canada and three from Latin America. Once we agreed that the symposium should take place in conjunction with the Annual Raptor Research Foundation (RRF) Conference in Seattle, we added five ex-officio members, made up of individuals representing RRF and/or coordinating the RRF conference's scientific program.

Hatching started on 13 November 1992 in the form of the symposium. It consisted of eighteen paper presentations and seven posters, and was attended by 130 individuals. On the following day, hatching was consummated with a workshop that addressed the most pressing management and research needs associated with this species. The workshop was a wonderfully serendipitous event, taking advantage of the presence of many of the world's most knowledgeable burrowing owl conservation biologists.

Objectives. The objectives of the symposium and workshop were to: (1) share information; (2) identify the most pressing management and research needs; and (3) take a significant step toward an action plan for this species.

What Follows. A paper on the taxonomy of the burrowing owl sets the stage for our task of understanding this species' needs. Three invited papers follow and give the reader a review of the status of the burrowing owl; an overview of the literature, based primarily on a review of the citations provided in Appendix A; and the results of the above Burrowing Owl Workshop, which followed the symposium.

The next section of this document is the symposium proceedings, *per se,* and includes both updated and expanded oral and poster presentations. These have been divided, somewhat arbitrarily, into population ecology and status, genetics and breeding biology, management, and other issues.

Finally, an attempt was made to provide as comprehensive a list as possible of relevant references (Appendix A). As admitted "bibliophiles" (a term I first heard from Butch Olendorff), we recognize how quickly such lists can become out-of-date. Hopefully, however, this product will become a springboard that will help propel future efforts toward the goal of proper environmental management for the burrowing owl.

Thanks. Thanks go to Paul James, Joe Schmutz and others who encouraged me to move forward on this project, and to all the authors, peer reviewers and the following members of the Steering Committee: Jack Barclay, Isabel Bellocq, Steve Brechtel, Richard Clark,* Mike Collopy,* Ken De Smet, Orville Dyer, Fabian Jaksić, Paul James, Brenda Johnson, Jeffrey L. Lincer, James MacCracken, Kay McKeever, Carl Marti, Brian Millsap, Richard R. Olendorff, John Pierce, Claire Puchy, Joe Schmutz,* Steve K. Sherrod, Mark Stalmaster,* Sergio Tiranti, Lenny Young,* and Brian Walton.

Finally, thanks and hearty acknowledgments go to those who, in a variety of important ways, supported this publication: The Raptor Research Foundation for making it easy to assemble many of the world's most knowledgeable burrowing owl biologists and managers, Sweetwater Environmental Biologists, Inc., The National Biological Service, World Wildlife Canada, The Denver Museum of Natural History, and the state of Florida's Nongame Program for financial assistance; my co-editor, Karen Steenhof, for her much-needed assistance, Joan S. Clark for proofreading skills beyond my comprehension and Sean Klope, for his word processing support; Allen Press for their guidance; and finally, my wife Carolyn for giving up many of "our" evenings and weekends in order that these proceedings see the light of day.

Jeffrey L. Lincer, Chair
Burrowing Owl Symposium

* Ex-Officio Members.

INVITED PAPERS

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CURRENT STATUS OF THE BURROWING OWL IN NORTH AMERICA: AN AGENCY SURVEY

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ABSTRACT.—The current status of the burrowing owl (*Speotyto cunicularia*) in North America (excluding Mexico) was assessed by mailing a questionnaire to the wildlife agencies of the 24 states and provinces in which burrowing owls breed. Each agency was asked to estimate, to the nearest order of magnitude, the size of its breeding population and to indicate whether or not the population was stable, increasing, or decreasing. In addition, each agency was asked to identify limiting factors affecting burrowing owls, and to indicate whether any special status was given to the species. Of the 24 jurisdictions, 11 (46%) reported a population between 1000 and 10 000 pairs, and 8 (33%) reported a population between 100 and 1000 pairs. Thirteen (54%) reported that their owl population was probably declining, and no agency reported an increase. Habitat loss (83% of respondents), reduced burrow availability due to rodent control (54%), and pesticides (46%) were the most important limiting factors identified. Sixteen (67%) of the jurisdictions give burrowing owls special status above that of regular protection.

KEY WORDS: *burrowing owl*; Speotyto cunicularia; *status*; *North America*.

Estado actual del tecolotito enano en Norte America: Encuesta de agencias

RESUMEN.—El estado actual del tecolotito enano (*Athene cunicularia*) en Norte America (excluyendo Mexico) se evaluo por medio de un cuestionario enviado por correo a agencias de fauna silvestre en 24 estados y provincias en las cuales el tecolotito se reproduce. A cada agencia se le pidio estimara, al orden de magnitud mas cercano, el tamaño de su poblacion reproductiva y que indicaran si la poblacion era estable, aumentaba, o disminuia. Ademas a cada agencia se le pidio identificara factores limitantes e indicara si la especie recibia alguna categoria especial. De las 24 juridicciones 11 (46%) reportaron una poblacion entre 1000 y 10 000 parejas y 8 (33%) reportaron una poblacion entre 100 y 1000 parejas. Trece (54%) reportaron que su poblacion de tecolotes estaba disminuyendo y nadie reporto un incremento en sus poblaciones. Perdida del habitat (85% de respondientes), reducido numero de madrigueras debido al control de roedores (54%) y pesticidas (46%) fueron los factores limitantes mas importantes que se identificaron. Diezyseis (67%) de las juridicciones le adjudican categoria especial al tecolotito enano ademas de la proteccion regular.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) is listed as Threatened in Canada (Wedgwood 1978, Haug and Didiuk 1991) and has been on the Blue List (Arbib 1971) in the United States since 1972. Despite this, accurate estimates and trends of burrowing owl numbers remain largely unavailable (Robbins et al. 1986, Root 1988). Analysis of Christmas Bird Counts from 1954–86 have indicated that the wintering population is generally stable, although a decline has taken place since the mid-1970s (James and Ethier 1989). Analysis of Breeding Bird Surveys from 1965–79 has shown only one significant change, an increase in the Glaciated Missouri Plateau Physiographic Region, covering parts of Saskatchewan, Alberta, Montana, North Dakota, and South Dakota (Robbins et al. 1986). Other es-

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Table 1. Results of the 1992 burrowing owl population survey.

Jurisdiction	Size[a]	Trend[b]	Factors[c]	Special Status
Alberta	low 4	D/S	H, Ps	Yes
Arizona	3	D	H, Ps, B	No
BC	1	D	H, Pr, B	Yes
California	4	D	H, Ps, Pr, Pe, B, V	Yes
Colorado	4	D	H, Ps, B	No
Florida	4	S	H, Pr, V	Yes
Idaho	low 4	S	H	Yes
Iowa	1	D/S	H, B, Ps	Yes
Kansas	3	D	B	No
Manitoba	2	D	Ps, Pr, Pe, V	Yes
Minnesota	1	S	B, V	Yes
Montana	3	S	?	Yes
Nebraska	3	D	H, Ps	No
Nevada	4	D	H, B, Ps	No
New Mexico	4	S	H, Ps	No
North Dakota	3	S	H, B, Ps	No
Oklahoma	3	S	H, B	Yes
Oregon	low 4	S	H, B	Yes
Saskatchewan	low 4	D	H, Ps, F	Yes
South Dakota	3	S	H, B	Yes
Texas	low 5	S	H, B	No
Utah	low 4	D	H	Yes
Washington	3	D	H	Yes
Wyoming	low 4	S	H	Yes

[a] 1 = 1–10 pairs, 2 = 10–100 pairs, 3 = 100–1000 pairs, 4 = 1000–10 000 pairs, 5 = 10 000–100 000 pairs.
[b] D = decreasing, S = stable.
[c] H = habitat loss, Ps = pesticides, B = reduced burrow availability, Pr = predators, Pe = persecution, V = vehicle collisions, F = food availability.

timates of breeding populations are largely nonexistent, so it was decided to conduct a survey of wildlife agencies to determine the current status of this owl in North America.

Methods

A questionnaire was mailed out to all 24 state and provincial wildlife agencies within the breeding range of the burrowing owl in North America. Four questions were asked in the form of a checklist: (1) What is, to the nearest order of magnitude (1–10 pairs, 10–100 pairs, 100–1000 pairs, etc.), the breeding population of burrowing owls in your jurisdiction?; (2) Is this population stable, increasing, or decreasing?; (3) What limiting factors are important in your breeding population?; (4) Does your jurisdiction provide burrowing owls with any special status? If so, what?

Results

All 24 wildlife agencies responded to the questionnaire (Table 1). Of these, 11 (46%) estimated their burrowing owl population at between 1000 and 10 000 pairs, and 8 (33%) estimated their population at between 100 and 1000 pairs. Only one (Texas) estimated a population of over 10 000 pairs, while the remaining four jurisdictions held between one and 100 pairs. However, despite these relatively healthy estimates of numbers, 13 (54%) reported that their owl population was probably declining, and no one reported an increasing population. Seven potentially limiting factors were identified. Of these, habitat loss (83% of respondents), reduced burrow availability due to rodent control (54%), and pesticides (46%) were the most important. Finally, 16 (67%) of the respondents give their burrowing owls some form of special status over and above that of regular protection.

Discussion

Although the total breeding population of burrowing owls in North America appears to be still relatively healthy, there is concern because over half of the jurisdictions reported declining populations (Table 1), and no one reported an increasing population. This is somewhat consistent with recent Christmas Bird Count analyses (James and Ethier 1989), but at odds with Breeding Bird Survey results for the period 1954–1986 (Robbins et al. 1986).

Factors such as habitat loss, reduced burrow availability, and pesticides were cited as important. Although studies of habitat selection by burrowing owls have been conducted (Rich 1986, Green and Anthony 1989, James et al. 1991), recent rates of conversion of grassland to cropland or urban development have rarely been reported. In Saskatchewan, e.g., between 1979 and 1986, 21% of the remaining grassland habitat was cultivated (Hjertaas and Lyon 1987). Clearly, more work is needed to determine recent and ongoing rates of conversion of burrowing owl habitat.

Some studies have also addressed the problem of reduced burrow availability (Hjertaas and Lyon 1987, Green and Anthony 1989, James et al. 1991). Although the use of strychnine for rodent control appears not to directly threaten burrowing owls (James et al. 1990), long-term removal of rodents will likely limit the availability of suitable burrows. This is likely to be particularly true with the already widespread but ongoing removal of prairie dogs (*Cynomys* spp.) in the United States (Miller et al. 1994). Studies on the direct impact of other pesticides are limited (James and Fox 1987, Fox et al.

1989, Fox and James 1991) and have shown that the use of carbofuran is detrimental to burrowing owls. More work is needed, however, on many other pesticides currently registered for use in the agricultural landscapes where burrowing owls often occur.

In summary, the burrowing owl in North America still appears to be quite numerous at present. However, it should be remembered that these data are derived from a questionnaire and few agencies have accurate counts. There is a great need for systematic surveys to be developed and conducted, particularly as over half of the agencies reported declining populations. More research is also needed on potentially limiting factors, and attention needs to be focused on agricultural policies throughout western North America that promote the destruction of native grassland habitat and its associated burrowing mammals.

ACKNOWLEDGMENTS

We thank all of the wildlife agency staff who took the time to complete the questionnaire. Work on burrowing owls has been supported by the Canadian Wildlife Service, FMC Canada, Nature Saskatchewan, Wildlife Habitat Canada, Wildlife Toxicology Fund, and World Wildlife Fund. B. Millsap, R. Olendorff, and K. Steenhof improved the manuscript. This paper is dedicated to the memory of Joanna Tudan-Sainberg.

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OVERVIEW OF LITERATURE ON THE BURROWING OWL

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ABSTRACT.—We examined titles for each of 845 burrowing owl (*Speotyto cunicularia*) citations included in the extensive bibliography prepared for this volume by R. Clark, J. Lincer, and J. Clark to determine year of publication, geographic locale of work, and topic reported. Although we readily admit that our review of citations is not an optimal approach to understanding the breadth of current knowledge about the burrowing owl, we believe our review provides a broad measure of the extent of work on different populations and facets of the biology of this species. Rate of publication of papers on the burrowing owl has been increasing since the early 1930s, with a rapid increase since the late 1970s. Most articles deal with the burrowing owl in North America (89% of all regional publications), and nearly half of North American papers were based on studies in Washington, California, or Florida. Burrowing owls in Mexico, Central America, South America, and the West Indies are vastly underrepresented in the literature for the species. Not surprisingly, there is a heavy subject bias in the published literature toward burrowing owl life history. There are surprisingly few papers dealing with conservation subjects, especially such topics as livestock grazing, pesticides, and land use impacts—issues that beg attention in today's environment.

KEY WORDS: *literature; burrowing owl;* Speotyto cunicularia; *trends.*

Revision de la litertura del tecolotito enano

RESUMEN.—Examinamos titulos de 845 citas del tecolotito enano (*Speotyto cunicularia*) incluidas en la extensa bibliografia preparada para este volumen por R. Clark, J. Lincer y J. Clark con fines de determinar el año de publicacion, localidad del trabajo y tema reportado. Aunque admitimos que nuestra revision de citas no fue de la manera mas optima para entender la variedad del conocimiento actual del tecolotito, creemos que nuestra revision provee una medida amplia de la extension de trabajos en diferentes poblaciones y facetas de la biologia de esta especie. La publicacion de articulos sobre el tecolotito enano ha incrementado desde principios de los años 1930's con rapido incremento desde fines de los años 1970's. La mayoria de los articulos tratan con el tecolotito en Norte America (89% de las publicaciones regionales) y casi la mitad de articulos Norte Americanos se basan en estudios realizados en Washington, California o Florida. El tecolotito enano esta mal representado en la literutura de la especie en Mexico, Centro America, Sud America e Indias Occidentales. Existe un zezgo hacia la literatura publicada sobre los habitos de vida del tecolotito enano. Existen pocos articulos que tratan con temas de conservacion, especialmente tales temas como el pastoreo de ganado, pesticidas, e impactos del uso de la tierra—temas que requieren atencion en el mundo de hoy.

[Traducción de Filepe Chavez-Ramirez]

The purpose of this paper is to present a brief overview of literature published through 1993 on the burrowing owl (*Speotyto cunicularia*). The basis for this summary is the exhaustive bibliography that has been assembled for this volume by R. Clark, J. Lincer, and J. Clark. We classified the references according to year, geographic locality, and subject matter based on information contained in

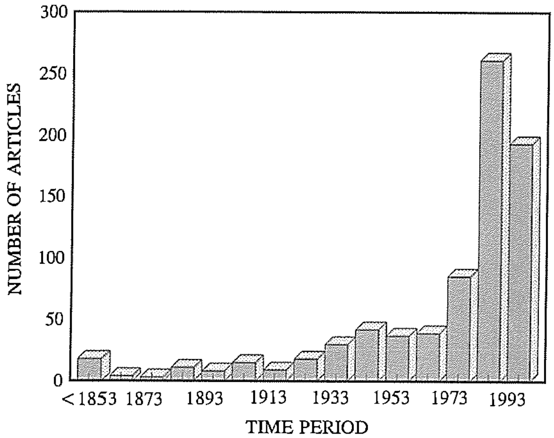

Figure 1. Distribution of burrowing owl publications by year.

the citation. In so doing, we have identified areas (both geographic and topical) that are both strongly and poorly represented in literature for this species.

METHODS

We converted a text file of the bibliography prepared by the above authors into a data base format with fields for author, year of publication, and title. We reviewed each entry and, according to information in the title, classified citations as to: (1) year of publication, (2) geographic area of work, (3) whether the publication was a scientific or popular article, (4) whether the article was specific to burrowing owls or dealt with more than one species, and (5) the major subjects (up to six) covered in the paper. Our analysis consisted of simple counts of citations by decade of publication, geographic area, article type, and subject. There are obvious limitations to this type of analysis, not the least of which is the possibility that the title may not adequately indicate the scope of the work reported. However, with cautious interpretation, we believe our analysis provides a useful overview of the literature for this species.

RESULTS

Temporal Distribution of Literature. As with raptor literature in general (Olendorff et al. 1980), the rate of publication of articles dealing with burrowing owls has increased in recent years (Fig. 1). Whereas the upswing in general raptor publications was not noticeable until the 1950s (Olendorff et al. 1980), the increase for burrowing owl literature began during the early 1930s with a strong second peak beginning in the 1970s. Clark et al. (1987) observed a similar 1930s upswing in the number of publications on nine other species of owls, based on 6590 articles listed in Clark et al. (1978). The slight downward trend in the number of burrowing owl articles in the most recent decade is probably an artifact of incomplete sampling of recent journals, particularly those published in late 1993. The recent emphasis toward more long-term studies might also contribute to this trend.

Geographic Distribution of Literature. Of 845 citations examined, 219 referred to issues different from ecology (e.g., physiology), where the place of the study was considered unimportant, or had no information on where the study was conducted. Nine publications referred to the world population (e.g., general books), and nine involved more than one country in different continents (e.g., comparative studies).

A total of 685 titles was assigned to geographic areas. North America accounted for 613 (89%), South America 41 (6%), Central America (including the West Indies) 23 (3%), and the rest of the world 8 (1%) (Fig. 2). Of the North American countries, 504 (82%) citations referred to burrowing owl populations in the United States, 84 (14%) in Canada, 5 (1%) in Mexico, and 20 (3%) referred to more than one North American country (Fig. 2). In South and Central America, most contributions came from Argentina, West Indies, Peru, and Chile (Fig. 3).

Many burrowing owl publications referenced populations throughout the United States and Canada. From the citations considered here, 373 were specific to a particular state in the United States while 131 referred to either more than one state or the country. Nearly half of the studies in the United States referred to burrowing owls in Washington, California, or Florida (Fig. 4). In Canada, 23 titles referred to the country or involved more than one province. The remainder of articles were nearly equally distributed among Saskatchewan (19 publications), British Columbia (18 publications), Manitoba (14 publications), and Alberta (10 publications).

Topical Distribution of Literature. We determined subject categories for 757 of the 845 literature citations in the bibliography. The 88 citations omitted were written for popular audiences and were too broad in scope to classify meaningfully. Each citation included in this analysis was classified into one or more of five major and 48 specific subject categories (Table 1).

Nearly all articles in the bibliography dealt with one or more aspects of burrowing owl life history.

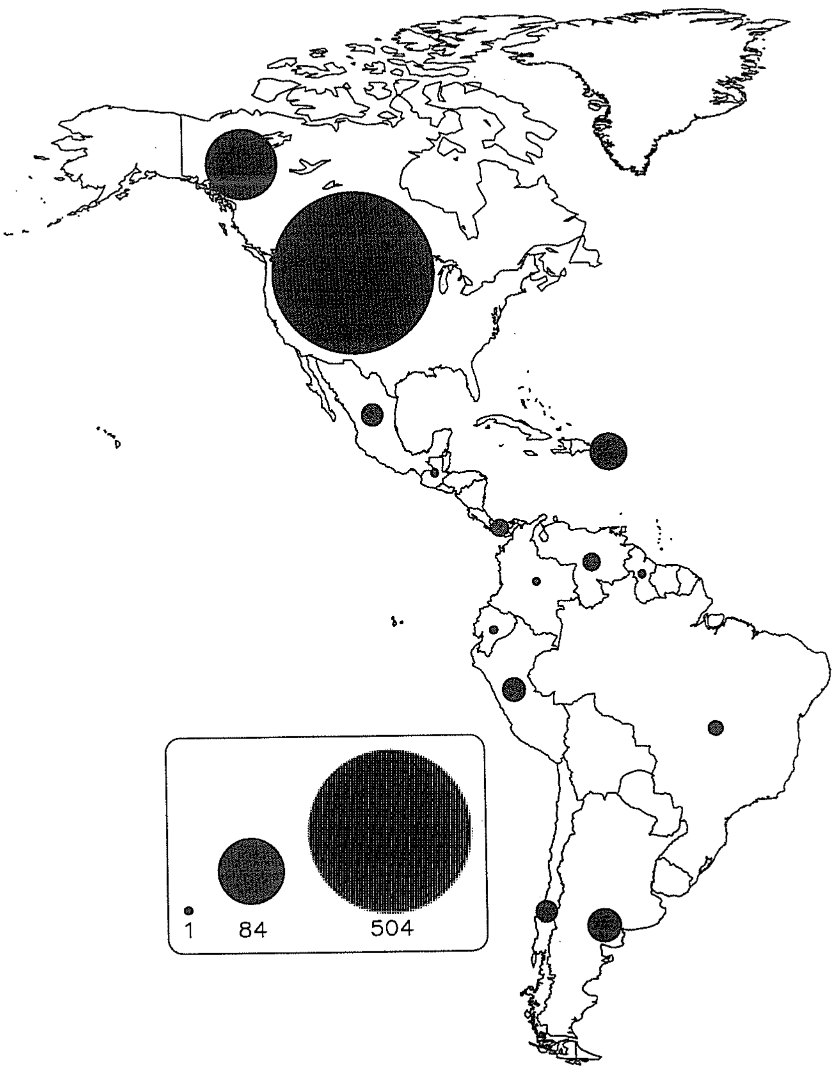

Figure 2. Geographic distribution of burrowing owl work in America. Circles are represented in square root proportion of the number of articles. Countries of the West Indies are represented in one circle for convenience.

The most prevalent topic was distribution, a category that included a large number of records of extralimital or unusual occurrence. General ecology, food habits, broad life history, physiology, and reproduction were other life history topics frequently reported on in the literature. Conservation and management topics comprised the next largest block of subject categories; within this broad area there were no specific categories, except general conservation, that stood out. Population status and technique papers occurred in about equal numbers in the bibliography. We were unable to classify 7% of all citations reviewed to a subject category based on the title.

DISCUSSION

Although our methods were not optimal, we believe our review provides a broad measure of the extent of work on different populations and facets of the biology of the burrowing owl. For example, it is clear that there has been a heavy bias in burrowing owl research toward populations in western

Table 1. Topical distribution of literature for the burrowing owl, based on a review of 774 scientific publications included in the burrowing owl bibliography (this volume).

MAJOR SUBJECT / SPECIFIC SUBJECT	NUMBER (%) OF PUBLICATIONS
Conservation/management	117 (15%)
Artificial burrows	5
Artificial perches	2
Broad conservation	46
Disturbance	4
Endangered species	16
Human dimensions	6
Land use	2
Management plans	9
Oil and gas impacts	1
Pesticides	8
Prescribed fire	1
Rehabilitation	6
Reintroduction	6
Relocation	3
Urban wildlife	2
Life history	765 (99%)
Disease	3
Behavior	19
Distribution	349
Ecology	39
Eggs	5
Food habits	67
Habitat	8
Gen. life history	90
Migration	8
Molt	7
Mortality	4
Mutualism	1
Paleontology	8
Parasitism	12
Physiology/anatomy	56
Reproduction	69
Roosting	1
Sexual dimorphism	3
Soils	2
Taxonomy	9
Vocalizations	5
Population status	71 (9%)
Abundance	7
Census	19
Populations	15
Status	30
Techniques	58 (7%)
Banding	6
General	10
Identification	25
Public relations	3
Statistical methods	1
Survey	8
Trapping	5
Unknown	51 (7%)

North America. Burrowing owl populations in Mexico, the Caribbean Islands, Central America, and South America remain relatively unstudied (Fig. 2). These populations differ from those in western North America in several ways (e.g., their tendency to excavate burrows in the Florida and Caribbean populations [Haug et al. 1993]), and should prove fruitful subjects for additional work. Not surprisingly, there is a heavy subject bias in the published literature toward burrowing owl life history. There are few papers dealing with conservation subjects, especially such topics as livestock grazing, pesticides, and land use impacts. These areas would seem to be worthy of additional emphasis.

Although over 800 articles have been written on the burrowing owl, one might still wonder how much we actually know about the species, and how critical our lack of information is for the conservation of this species. The high and increasing rate

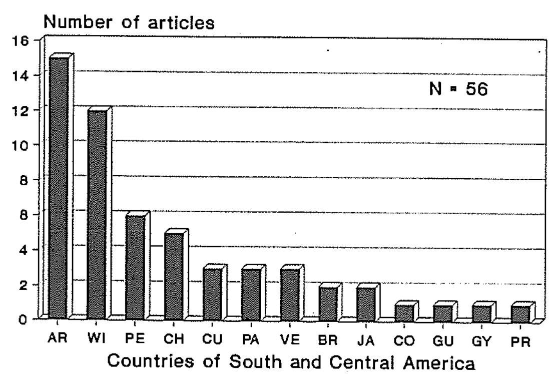

Figure 3. Number of articles on burrowing owl populations in South and Central American countries: AR = Argentina, BR = Brazil, CH = Chile, CO = Colombia, CU = Cuba, EC = Ecuador, GU = Guatemala, GY = Guyana, JA = Jamaica, PA = Panama, PE = Peru, PR = Puerto Rico, VE = Venezuela, WI = West Indies (excluding Cuba, Jamaica, and Puerto Rico).

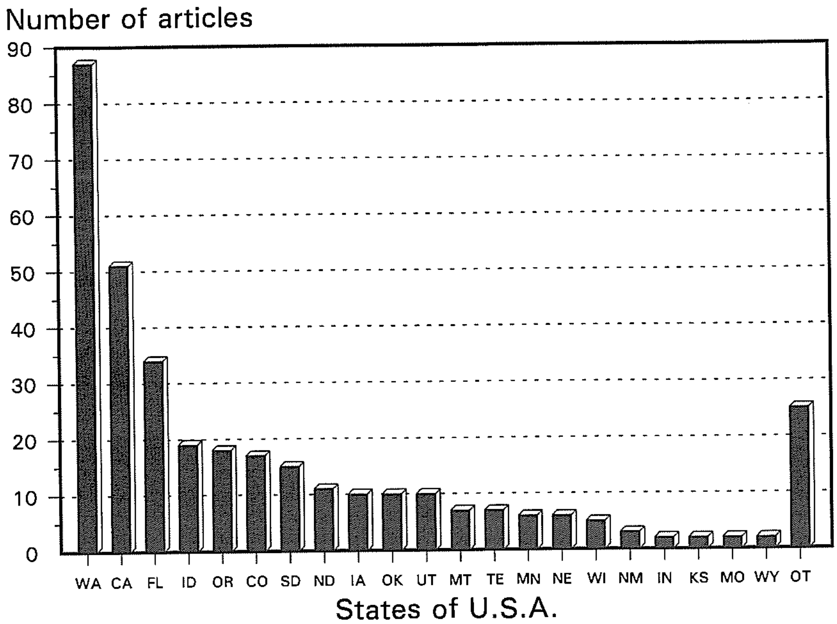

Figure 4. Number of articles on burrowing owl populations in different states in the United States. OT refers to others.

of publication of articles dealing with this species is a positive sign that existing information gaps will continue to narrow.

ACKNOWLEDGMENTS

Our analysis would not have been possible without the painstaking bibliographic work of R. Clark, J. Lincer, and J. Clark; we thank them for sharing their data with us. The manuscript was improved considerably by the reviews of K. Steenhof, R. Clark, and J. Lincer.

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J. Raptor Res. Report 9:11–13

TOWARD AN ACTION PLAN

THE RESULTS OF THE BURROWING OWL WORKSHOP, 14 NOVEMBER 1992, BELLEVUE, WASHINGTON

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ABSTRACT.—A workshop was held after The First International Burrowing Owl (*Speotyto cunicularia*) Symposium and in conjunction with the 1992 Raptor Research Foundation Conference. This workshop had the following goals: (1) identify and prioritize burrowing owl problems and issues; (2) determine if solutions are known; and (3) propose necessary research to address remaining problems and issues. Using the Nominal Group Process and brain-storming committees, approximately 40 biologists and wildlife managers addressed the above goals in a synergistic and productive way.

KEY WORDS: *burrowing owl*; Speotyto cunicularia; *issues*; *problems*; *solutions*; *research*.

Hacia un plan de accion, los resultados de un taller sobre el tecolotito enano, noviembre 14 1992, Bellevue, Washington

RESUMEN.—Un taller se realizo despues del Primer Simposio Internacional del Tecolotito Enano (*Speotyto cunicularia*) y en conjunto con la conferencia de 1992 del Raptor Research Foundation. Este taller tuvo las siguientes metas: (1) Identificar y ponerle prioridades a los problemas y situaciones del tecolotito enano; (2) Determinar se se conocen soluciones y; (3) Proponer investigacion necesaria para afrontar problemas y situaciones restantes. Usando el Proceso de Grupo Nominal y comites de discussion, aproximadamente 40 biologos y manejadores de fauna afrontaron las metas propuestas de una manera conjunta y productiva.

[Traducción de Filepe Chavez-Ramirez]

The First International Burrowing Owl (*Speotyto cunicularia*) Symposium was held 15 November 1992, in conjunction with the Annual Raptor Research Foundation Conference in Bellevue, Washington. The symposium drew together scientists and managers from throughout North, Central, and South America. This unique assemblage of some of the world's most knowledgeable burrowing owl biologists afforded the opportunity to discuss and share information relevant to burrowing owl biology, conservation and management. This workshop provided a forum for the definition and discussion of contemporary issues affecting burrowing owls.

GOALS

The goals for this workshop were to identify and prioritize burrowing owl problems and issues; determine if solutions to the above are known; and to propose the research necessary to address those problems for which solutions are not apparent.

METHODS

After a brief review of the previous day's Burrowing Owl Symposium by Brian Millsap and M. Isabel Bellocq, the group was introduced to the Nominal Group Process (NGP). This is a structured process developed by the Rand Corporation to maximize and rank input from a group of knowledgeable participants.

The steps to address the first goal (i.e., identifying problems and issues) involved the standard NGP approach: (1) a silent generation of ideas by each participant; (2) a listing of cumulative ideas by all participants; (3) a discussion of these ideas (for clarification only); and (4) ranking ideas by giving each participant four votes to be distributed over all proposed ideas. The final "rank" is the sum of participant votes assigned to each of the issues and needs.

The remaining goals (i.e., identifying known solutions and necessary research) were assigned to two brainstorming committees which were chaired by Jack Barclay and Robert Lehman, respectively.

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RESULTS

Issues and Needs. The group identified the following issues and needs, during the NGP, as important to the conservation and management of the burrowing owl. These have been ranked from highest to lowest priority by the workshop participants. Minor changes for clarification, and consolidation of similar issues, have been made by the author.

1. General Population Decline Throughout Entire Range.
2. Habitat Loss and Degradation (emphasis placed on total needs, including discing for fire, land use activities, and habitat conversion) Leading to Population Fragmentation and Associated Genetic Problems.
3. Identifying Wintering Areas/Understanding Wintering Ecology/Establishing International Agreements.
4. Decline of Burrowing Mammals (discussion focused on government-sponsored animal damage control programs)/Need for Better Understanding and Management of Prairie Dog and Badger.
5. Public Education, Including Education of Land Managers and Policy-Makers/Encouraging Private Landowner and Public Participation in Protecting Habitat/ Recognizing the Problems of Overloading Demands on Landowners.
6. Prioritizing Issues (include elevated level of strategy, role of biologist, and ecosystem management).
7. High Adult Mortality/Mortality (especially of young) by Vehicles/Mortality of Females and Chicks (from development and associated earth moving).
8. Lack of Standardized Survey Protocols, Reproductive Data, Population Status and Information on Specific Causes of Decline.
9. Effects of Agricultural Chemicals and Other Toxics.
10. Government Policy that Rewards Destruction of Habitat, Lack of National/ Federal, State and Local Regulatory Mechanisms (for native and disturbed habitat).
11. Lack of Behavioral Information, Including Foraging Strategies, Range, Dispersal of Young and Effectiveness of Translocation and/or Relocation.

Known Solutions. The focus of the Solutions Committee was to identify approaches that have already proven productive in the wildlife/people management arena. This group concluded that there were four subject areas into which their findings could be divided: (1) protection of habitat; (2) management of habitat; (3) standardization of survey methods; and (4) reduction of mortality.

This committee emphasized that protection of habitat should include protection of breeding, wintering, foraging, and migration habitats. Mechanisms to accomplish the above protection include: developing and enforcing sound legislative/governmental policy at all levels, including statutes, ordinances, laws, subsidies, and treaties; educating the public to support the above policies; enlisting participation from public and private landowners; and acquiring/protecting priority habitat through fee simple, conservation easement, transfer of development rights or other mechanisms.

Discussions on management of habitat emphasized that management should occur at all levels, from the backyard to the community and ecosystem. Successful mechanisms to manage habitat include: providing education that addresses key habitat components (i.e., burrowing mammals, vegetation, and human activities/land use). In connection with this, the committee created a resolution for the protection of burrowing mammals, which was submitted to, and passed by, the RRF membership for approval (see *Journal of Raptor Research* 27(1):52); and providing financial incentives which would result in avoiding or minimizing the impact of land use on the burrowing owl. For instance, user fees could be charged as a disincentive to a land use which would impact burrowing owl biology. Conversely, incentives could be in the form of a payment to a landowner for not disrupting burrowing owl habitat. An extension of this concept would be payments to a landowner to encourage the protection or establishment of suitable habitats.

Standardized survey methods are critical to assessing the status of a species across its range. Without proper survey protocol and mitigation guidelines, cumulative impacts go unnoticed and opportunities for meaningful mitigation are lost. To address this need, a group called the California Burrowing Owl Consortium recently prepared the "Burrowing Owl Survey Protocol and Mitigation Guidelines." This document is included in these proceedings as Appendix C. These useful suggestions are provided for review and comment but they have not as yet been given any official status.

Mortality can be reduced at several levels, but the following were identified as important mortality factors that should be addressed in any way reasonable: automobile collisions, toxic substances and exogenous organisms (e.g., red foxes (*Vulpes vulpes*) and feral dogs and cats).

Necessary Research. The Research Committee logically concluded that two main threats or proximate factors contribute to population declines—fecundity problems and mortality factors. In part, these threats/factors occur: (1) due to habitat modification or loss within both breeding and wintering ranges (and associated effects on vegetation and prey and burrow availability); (2) during movements (dispersal and migration); and (3) because of genetics (isolation and inbreeding suppression).

The committee concluded that the following prioritized research is needed throughout the species' range:

1. Conduct population surveys (counts) to assess the species' current status;
2. Standardize species-specific terms to facilitate communication between researchers (especially terms relating to reproductive biology);
3. Monitor reproductive success;
4. Identify important mortality factors (both seasonally and geographically);
5. Characterize and inventory habitat (include use of gap analysis to identify important habitats that may require protection);
6. Identify migratory and dispersal patterns;
7. Develop research technology (e.g., radiotelemetry) to improve data collection; and
8. Conduct local demographic studies to determine patterns of population increase, decline, and persistence, and relate patterns to genetic and other influences.

CLOSING

The above ideas and recommendations represent the outcome of a synergistic process involving many dedicated wildlife biologists and environmental managers. The listings are not exhaustive and the author encourages the reader to review the individual papers that follow. In many cases, the authors have recommended management techniques and/or necessary research. The results of the First International Burrowing Owl Workshop and the recommendations of the symposium authors should be taken in concert to develop population-, regional-, and range-level action plans.

ACKNOWLEDGMENTS

This work was supported by Sweetwater Environmental Biologists, Inc. and BioSystems Analysis, Inc. I appreciate both Jack Barclay and Robert Lehman chairing the Known Solutions and Necessary Research Committees on the spur of the moment. This manuscript was reviewed by, and benefited from, the comments of Jack Barclay, Robert Lehman, Mike Collopy, Brian Millsap and Karen Steenhof. I am particularly indebted to the workshop participants: Wendy Aeschliman, Ursula Banasch, Jack Barclay, Sean Barry, David Beig, M. Isabel Bellocq, Janis Buchanan, Gene Butellio, Rebecca Cull, Trish Cutler, Penelope Delevoryas, Dave DeSante, Fred Dobler, Leora Feeney, Lisa Fitzner, Denis Flath, Greg Green, Jerry Hickman, Dale Hjertaas, Geoff Holroyd, Brenda Johnson, Shirley Kendall, Robert Lehman, Jeffrey L. Lincer, Mike Mackintosh, Mark Martell, Carl Marti, Kay McKeever, Brian Mealey, Brian Millsap, Joan Priest, Claire Puchy, Eric Ruhlen, John Schladweiler, Joe Schmutz, Karen Steenhof, Lynne Trulio, Sigrid Ueblacker, Roger Wallace, Troy Wellicome.

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A REVIEW OF THE TAXONOMY AND DISTRIBUTION OF THE BURROWING OWL (*SPEOTYTO CUNICULARIA*)

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ABSTRACT.—The burrowing owl, traditionally, has been widely distributed in both the temperate and tropical xeric grasslands and shrub communities of the Western Hemisphere. Within the Caribbean region at least two of its geographic races have become extinct within historic times. This article summarizes the available information on the anatomical measurements and notes the generally larger size of individuals of continental populations versus island populations. Distributions with regard to the species are presented by geographic races. Areas where the populations are declining are noted; e.g., southern British Columbia, Alberta, Saskatchewan, and Manitoba and regions of California. Uniquely, the race *floridana* of the state of Florida and the Bahama Islands is expanding or recolonizing areas formerly inhabited, at least in Florida.

KEY WORDS: Athene cunicularia; *burrowing owl*; Speotyto cunicularia; *taxonomy*; *distribution*.

Una reseña de la taxonomía y distribución del Speotyto cunicularia

RESUMEN.—Tradicionalmente, el Búho Madriguero ha estado localizado tanto en las zonas templadas y tropicales como en las comunidades con arbustos dentro del Hemisferion Occidental. Por lo menos dos de sus razas geográficas se han extinguido a través del tiempo dentro de la región del Caribe. Este documento sintetiza la información disponible con respecto a las medidas anatómicas e indica la diversidad de tamaños individualtes en las poblaciones continentales contra las poblaciones de las islas. La distribución de las especies son presentadas de acuerdo a las razas geográficas. Areas donde las poblaciones han declinado, son: al Sur de British Columbia, Alberta, Saskatchewan, Manitoba y las regiones de California. La raza *floridiana* de la Florida y de las Islas del Bahamas, especialmente se ha expandido o ubicado en áreas anteriormente deshabitadas en la Florida.

[Traducción de Filepe Chavez-Ramirez]

Researchers have suggested, among other taxonomic relationships, that the burrowing owl is most appropriately classified within the monotypic Genus *Speotyto* or that it is a long-legged species of *Athene*.

The burrowing owl is widely distributed within grasslands, low-growth shrub, and deserts in the Western Hemisphere. Formerly distributed from the prairie provinces of western Canada to Tierra del Fuego, it has been retreating from both the northern and southern extremes of its range. It has been extirpated from the southern tip of its range and some of the islands of the Carribbean Sea where suitable habitats formerly existed.

METHODS

The material for this review was collected in conjunction with preparations for the production of a revised edition of Clark et al. (1978) working bibliography of owls of the world. Specimens were examined in the museums of Kansas University in Lawrence, the Peabody Museum at Yale University, Louisiana State University in Baton Rouge and the Field Museum in Chicago. Libraries associated with those museums were also checked for appropriate literature. Literature was also acquired for the compilation of a bibliography on the burrowing owl that appears elsewhere in this publication.

TAXONOMY

The burrowing owl was originally ascribed to the Genus *Strix* by Molina (1782) being named *Strix cunicularia*. It underwent a number of name changes (see Strickland [1855], Ridgway [1914] and Peters [1940] for synonyms) until Gloger (1842) placed it in the monotypic genus *Speotyto* in which it remained until moved into *Athene*. Meinertzhagen (1951) had suggested that, based on both anatomical and behavioral characteristics, *cunicularia* be included with *Athene*. He pointed out that *Athene brama* and *Athene noctua*, like *Athene cunicularia*, are "known to breed underground, sometimes in association with snakes and rodents." He also noted that he had observed both *A. brama* and *A. noctua* "excavating with vigour in earth." He further noted that in both genera the nostrils are swollen in a fresh state but the nostril aperture is slightly differently placed in the burrowing owl than in the other two species of *Athene.* Other suggested differences were less tarsal feathering in the burrowing owl with hairs extending to the ends of the toes but lacking on the back of the tarsus. He noted that in some races of *Athene noctua* the hairs may be exactly as in the burrowing owl but that the back of the tarsus is always feathered in that species. Meinertzhagen (1951) also pointed out that the fifth primary in *Athene* is usually distinctly notched but sometimes scarcely perceptible and in the burrowing owl the notching on the outer web of the fifth primary is absent but sometimes slightly suggested. While Sibley and Monroe (1990) stated that "DNA-DNA hybridization evidence indicates that this species [i.e., *Speotyto cunicularia*] is not closely related to *Athene,*" Sibley (pers. comm.) acknowledged that in their work they "were not trying to resolve the precise pattern of branching among species within a group" but were rather looking at the older branches on the evolutionary tree. Schmutz and Moker (1991) state, based on cytogenetic evidence, that the "former distinct status [i.e., of being a monotypic Genus *Speotyto*] may be more appropriate." They suggest that the burrowing owl karyotype may be a relatively primitive species with characteristics having closer affinity to an ancestral owl species than that of the other species of *Athene.* Olson and Hilgartner (1982) indicated that *Speotyto* has been separated from *Athene* based on the "greatly lengthened tarsometatarsus, correlated with the highly terrestrial and fossorial habits of the bird." In additon, they pointed out that in the absence of other osteological differences it was better to emphasize the similarities rather than the differences by including *cunicularia* with *Athene.* Ford (1966) recommended inclusion of *cunicularia* within *Athene* based on osteological considerations. Scherzinger (1988) has made a strong case for "cancellation of the genus *Speotyto* and the assimilation of the burrowing owl in the genus *Athene*" basing his recommendation on careful comparisons of vocalizations.

Speotyto cunicularia is widely distributed where there are stretches of open land in arid and semiarid climates but also in wetter climates. Ford (1966) reported fossil remains of an extinct species

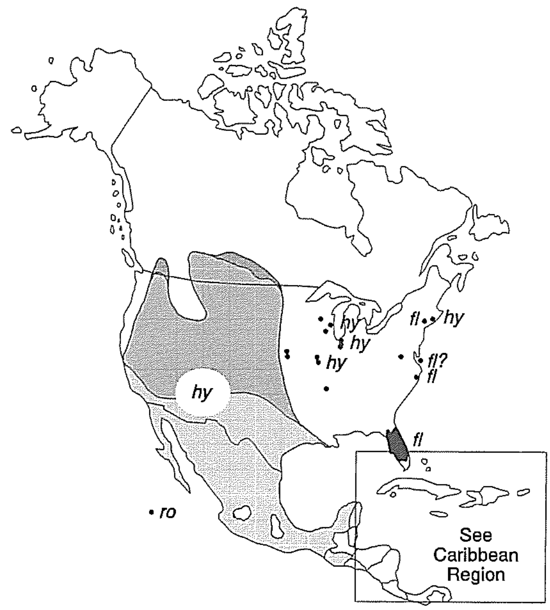

Figure 1. Distributional range of the races *hypugaea* (hy), *floridana* (fl) and the island race *rostrata* (ro). Dark shading at the northern limits of *hypugaea* indicates areas of declining numbers. The next lighter shading is the breeding range from where most birds would be expected to migrate for the winter period, south of which they are permanent residents (lightest shade).

of owl *Speotyto megalopeza* "which appears to have been very similar to the modern *Speotyto cunicularia,* differing most notably in being more robustly built," from Upper Pliocene deposits in Meade County, Kansas. Ford and Murray (1967) reported a fossil of *Speotyto megalopeza* from Upper Pliocene (3.48 ± 0.27 million years B.P.) that came from Twin Falls County, Idaho. Voous and Cameron (1988) speculate that the Old World little owl (*Athene noctua*) is an early descendant and colonist from North America, perhaps in early post-Tertiary times. Lundelius et al. (1983) indicate *Speotyto cunicularia* from archeological sites in California and New Mexico from the Late Pleistocene and Steadman et al. (1984) recorded fossils of it from the time period 4300 to 2500 yr B.P. from Antigua (Lesser Antilles) and indicated they were of the recently extinct race *amaura* (last collected in 1890, Cory 1891). Olson and Hilgartner (1982) noted fossil remains of the burrowing owl from Jamaica, Barbuda, Mona and Cayman Brac, four islands where it no longer exists. Geographic races are listed below chronologically; i.e., according to the

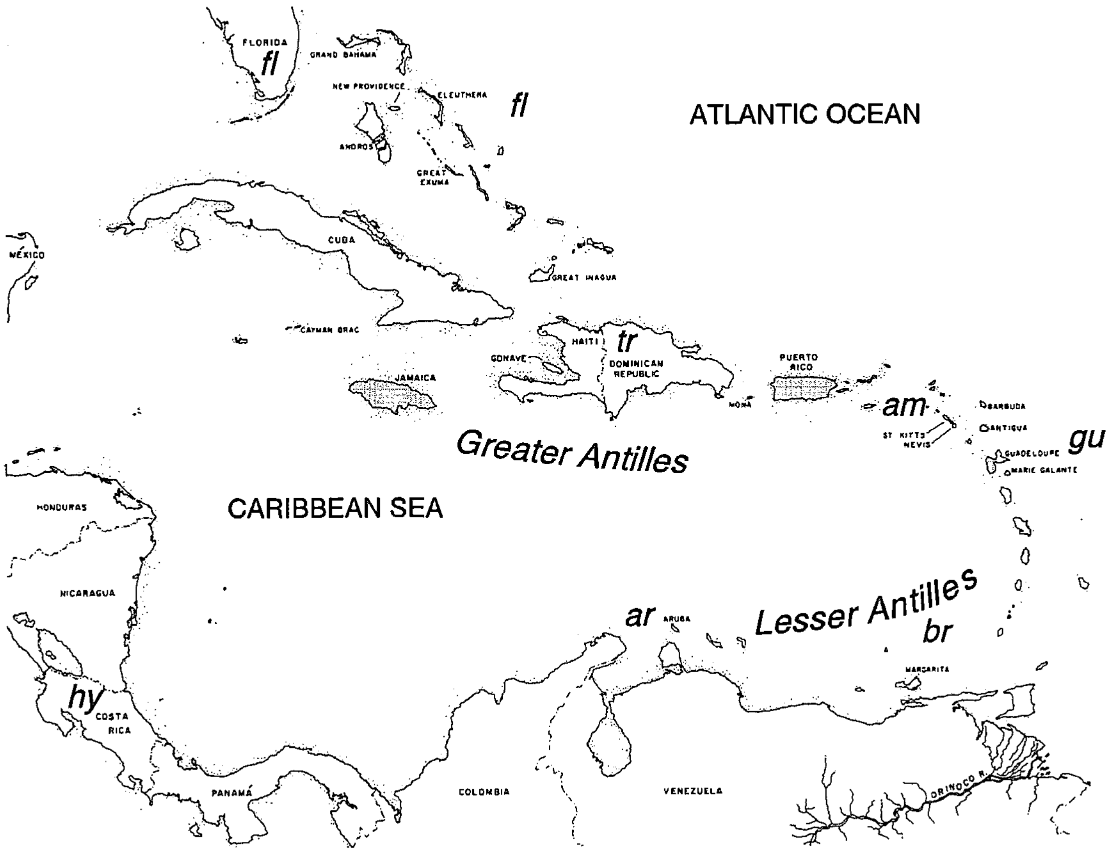

Figure 2. Distributional (or former) ranges of the races *troglodytes* (tr), *amaura* (am) extinct, *guadeloupensis* (gu) extinct, *brachyptera* (br) (this race is known to exist on mainland Venezuela) and *arubensis* (ar) (known only from Aruba Island). All islands named have had or presently have populations of the burrowing owl except they are known to no longer exist on Cayman Brac, Jamaica, Mona, Puerto Rico, Barbuda, St. Kitts, Nevis, Antigua, Guadeloupe, and Marie-Galante. Shading indicates those islands where it has been extirpated or become extinct. Researchers/observers of the other islands should watch carefully for their presence.

date of original description. Their approximate geographic distributions are shown in Figs. 1, 2 and 3 and include the following:

cunicularia (Molina 1782)—Chile from Tarapacá to Cautín; southern Bolivia; Paraguay; Uruguay; southern Brazil in State of Rio Grande do Sul; Argentina south to Tierra del Fuego. In Chile, along the coasts and the sparsely vegetated hillsides of the Andean foothills up to about 1524 m (5000 feet), from Tarapacá south to Valdivia (Johnson 1967). Throughout Argentina from the plains and foothills of Patagonia to the Chaco and pre-puna of the northwest where Olrog (1976) described the race *partridgei*. It is likely extirpated from Tierra del Fuego since the early 1920s (Humphrey et al. 1970). It was probably common in the northern, nonforested portion of the island and its disappearance coincided with widespread sheep-grazing and may have resulted from sheep trampling the burrows.

grallaria (Temminck 1822)—dry interior of Brazil from Maranhão and Piauhy southward through Goyaz and Bahia to southeastern Matto Grosso and Paraná.

hypugaea (Bonaparte 1825)—southern British Columbia east to central Manitoba, south along the eastern edge of the Great Plains, and south to western Panama. James (1992) presented strong evidence that Canadian birds winter at least as far south as Central America and James and

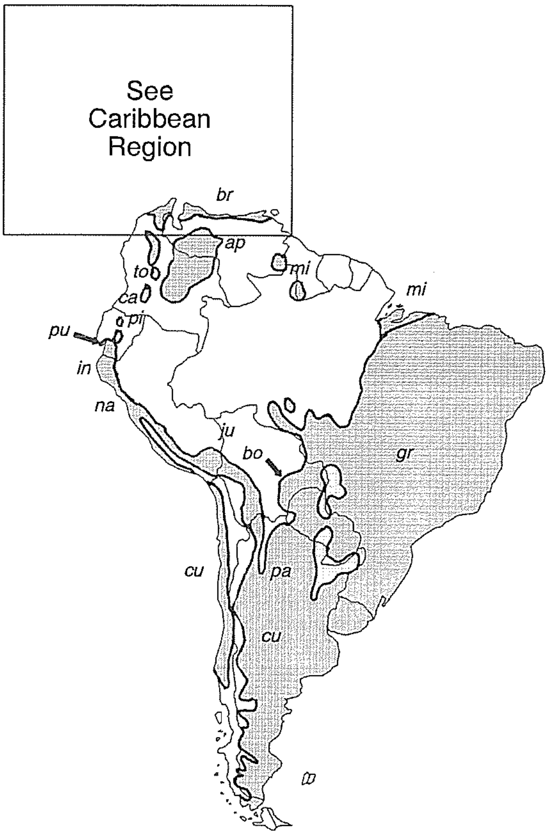

Figure 3. Distributional range of the races *apurensis* (ap), *boliviana* (bo), *brachyptera* (br), *carrikeri* (ca), *cunicularia* (cu), *grallaria* (gr), *intermedia* (in), *juninensis* (ju), *minor* (mi), *nanodes* (na), *patridgei* (pa), *pichinchae* (pi), *punensis* (pu), and *tolimae* (to). Much work is needed on the distributional range of many of these races and birds from areas of intergrading should be examined very carefully. Much information is needed from the field for most all races.

Ethier (1989) showed that their numbers have been declining steadily since the mid 1970s. Land (1970) suggested that "most, possibly all, Central American records seem to be of migrants from the north." Wetmore (1968) indicated that "stragglers reach western Costa Rica, and there is one record in Panamá . . . at Divalá, Chiriquí." Specimens found outside of the normal range, having been collected or seen and positively identified to be of this race are shown in Figure 1 and were from Wisconsin (Pelzer 1942, Wilde and Oar 1981), Illinois (Musselman 1931), Indiana (Hine 1924, Kirkpatrick 1942), New York (Bull [1974] stated that the individual, which was collected on Long Island, "may well have wandered from the west, but definite proof is lacking"–indicating that it may have been an escaped captive bird; Davis 1977, Richard 1988), Missouri (Easterla 1967), and Virginia (Duncan 1922, Lewis 1988). It should be noted that the determination of this last-mentioned bird, in Virginia, was based on the bird being "very pale compared to any illustrations of the Florida phase" that the author had seen and the "rather small bill, whereas the Florida phase is described as having a large bill for its size." Table 1 shows the *floridana* race as having a culmen about 2 mm longer than that of the western race *hypugaea* and the aforementioned author did not indicate that the bird was ever in the hand. The pattern of *floridana* birds along the Atlantic coast (see below) suggests that perhaps the birds might be "hitchhikers" on ships.

floridana (Ridgway 1874)—the prairies of central and southern Florida, Bahama Islands. Bond (1943) reports that he received notification of a bird of this race being taken at Campo Florido, Havana, Cuba. Barbour (1943) reported that he tried to collect two birds at the western tip of Grand Bahama and they "flew directly out to sea in the direction of Florida." A "careful search of several days duration . . . finally convinced me that these birds had probably shot right across to the mainland" (Barbour 1943). Betz (1932) reported it breeding on Hog Island off the west coast of Pinellas Co., Florida during 1929 through 1932. Neill (1954) reported the northward expansion of this race (to Ocala). Ligon (1963) reported it had continued to Gainesville and Chiefland and south into the Florida Keys (Marathon Key). Sprunt (1938) had reported a number of birds seen along the highway from Tavernier to Marathon (Lower Matecumbe Key, Long Key, Grassy Key and Key Vaca). Ligon (1963) pointed out that as fossil records of the species are recorded from Alachua and Marion Counties they are actually recolonizing former (prehistoric) range. Courser (1979) reported that they had been recorded breeding further north in Lafayette, Duval and Suwannee Counties. This recent range expansion has apparently been in response to large-scale clearing of forest for urban development and Millsap and Bear's (1990) reporting of double-brooding by this race indicates favorable breeding conditions. Pub-

Table 1. Anatomical measurements[a] of some burrowing owl races from museum skins (from Ridgway 1914 and Stone 1922).

Geographic Race	Sex	Sample Size	Length (Skins)	Wing	Tail	Culmen	Tarsus	Middle Toe
cunicularia	♂	5	[b]	179.5	86.6	16	47.3	21.7
	♀	5		181	83.7	15.5	46.8	21.7
hypugaea	♂	26	224	172.3	81.6	14.2	45.3	20.3
			(200–245)	(164.5–178)	(74.5–86)	(13–15)	(41.5–48.5)	(19–22)
	♀	33	223	170.3	79	13.9	43	19.5
			(205–250)	(162.5–181)	(71.5–85.5)	(13–15)	(40–46.5)	(18–20.5)
rostrata	♂	10	221	165	76.3	16.1	47.1	21.4
			(215–235)	(160–169)	(72–79.5)	(15.51–17)	(45.5–49)	(20–22.5)
	♀	2	198.5	164.2	70.2	16	45.2	20.7
			(195–202)	(164–164.5)	(70–70.5)	(15.5–16.5)	(44.5–46)	(20.5–21)
floridana	♂	10	216	164.2	76.4	14.9	44.1	20.6
			(195–230)	(154.5–170)	(73–80.5)	(14.5–15.5)	(42–46.5)	(18.5–21.5)
	♀	10	216	163.9	75.6	14.8	43	20.8
			(191–235)	(156–169)	(70–78.5)	(14–15.5)	(41–45.5)	(19.5–22)
troglodytes[c]	♂	6	211	157.2	73.9	15.2	42	20.5
			(200–230)	(153–161.5)	(72–76)	(14.5–15.5)	(38–45.5)	(19–21.5)
	♀	6	202	157	70.3	14.8	41.2	20.4
			(185–210)	(145–165.5)	(64.5–76.5)	(14–15.5)	(38.5–45)	(18.5–21.5)
brachyptera	♂	1	[b]	142	63.5	13.5	40	19
	♀	1		152	63.5	14.5	41.5	18
amaura	♂	3	211	150.7	73.3	14.2	40.8	20.5
			(200–227)	(145.5–154)	(70.5–75.5)	(14–14.5)	(39.5–41.5)	(20–21)
	♀	3	249	150	72	14.8	39.8	20.8
			(218–295)	(148.5–151)	(70–73.5)	(14.5–15.5)	(39.5–40.5)	(19.5–21.5)
guadeloupe	?	3	"about" 215	160	79.5	15.2	44.2	21.5
				(158–162.5)	(75.5–86.4)	(15–15.5)	(42.5–46.2)	
carrikeri[d]	?	1	[b]	173	78	14	46	

[a] All measurements in mm.
[b] Data not available from article.
[c] Listed by Ridgway as *S. f. dominicensis* also his text and tabled values do not agree. Text values used.
[d] Stone (1922).

lished records for this race in eastern United States north of Florida include a bird collected at Salvo, Dare County, North Carolina (Sykes 1974), a specimen (presumably of this race) taken just off the coast of Virginia outside of Hampton Roads (Strong 1922) and a bird, identified while in hand, was frequenting an area of Cedar Beach, Suffolk County, New York (Davis 1977). Sykes (1974) pointed out that the bird reported by Strong (1922), and a bird reported as boarding a sport-fishing boat 40 km off the east coast of Florida (Cocoa Beach, Brevard County, Florida) suggest that these northern sightings of *floridana* may be of birds that have moved to those areas, which are all coastal, by hitchhiking on boats. Sykes (1974) notes that "on the southeast coast of Florida the busy coastal shipping lane is within 1–2 km of shore."

guadeloupensis (Ridgway 1874)—Reported as formerly occurring either on the Island of Guadeloupe or Marie Galante in the Lesser Antilles (Peters 1940) and, while Bangs (1930) reported that "this bird really never occurred in Guadeloupe" so the original specimen must have been "from Marie Galante, a drier more arid isle nearby, where the species formerly occurred," a specimen in the Field Museum in Chicago (FMNH catalog number 40487) has listed as the locale of origin "Guadeloupe, West Indies." Extinct. Greenway (1967) indicates its former range as Marie Galante Island, West Indies.

amaura (Lawrence 1878)—Antigua, Nevis and St.

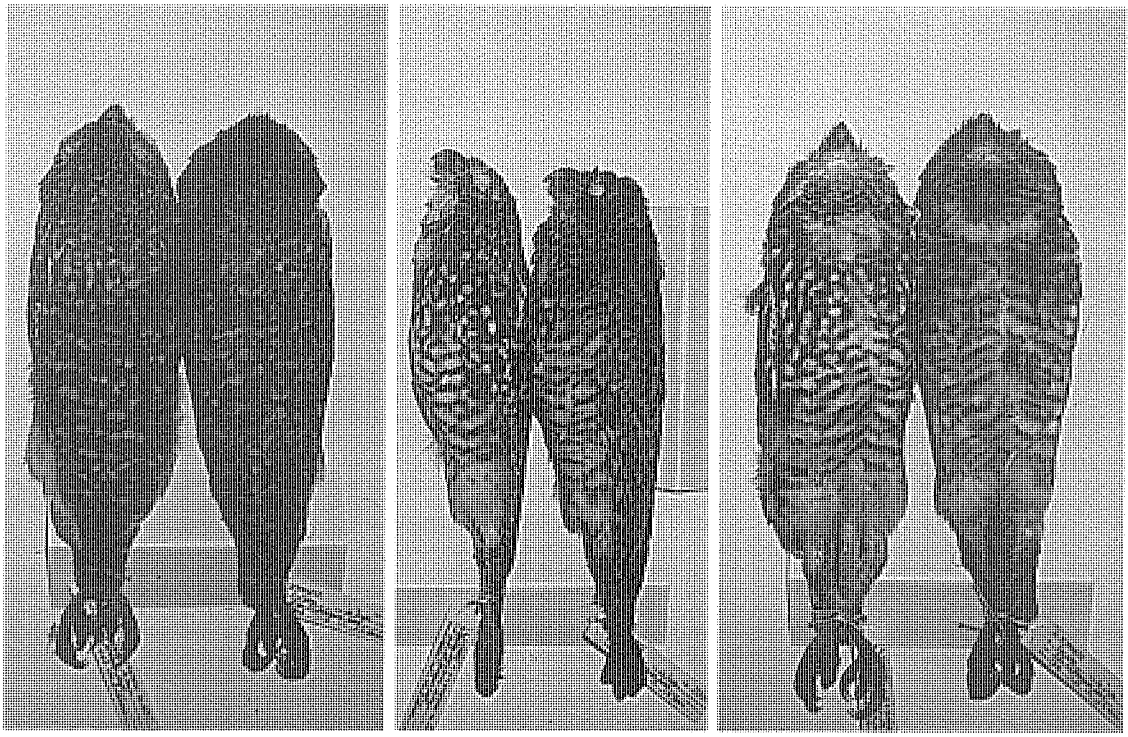

Figure 4. Two birds of the race *troglodytes* in the Louisiana State University (Baton Rouge) museum are interesting in that they show considerable difference in color. The gray bird (left) was a female (collection No. 6567) collected at about 610 m (2000 feet), 12 km northeast of Jarabacoa (Dominican Republic) on 31 October 1963. The rufous bird (right) (collection No. 7934) is a male collected in the same locale as the female on 17 July 1968.

Kitts (Pregill et al. 1988). Extinct. Danforth (1934) noted that this owl was said to have become extinct soon after the introduction of the mongoose.

troglodytes (Wetmore and Swales 1886)—Island of Hispaniola; Beata and Gonave Islands. Two birds of this race (see Fig. 4) in the Louisiana State University museum (Baton Rouge) are interesting in that they show considerable difference in color, a characteristic which is included in some racial descriptions. A gray bird was a female (collection No. 6567) collected at about 610 m (2000 feet), 12 km northeast of Jarabacoa (Dominican Republic) on 31 October 1963. A rufous bird (collection No. 7934) must have been collected in the same locale as the information on the label reads essentially the same except that it is a male collected on 17 July 1968. Does it indicate polymorphism or is one of the birds colored by the soils that it lived in (König pers. comm.)?

rostrata (C.H. Townsend 1890)—Isla Clarión (Clarion Island) off the west coast of Mexico.

nanodes (Berlepsch and Stolzmann 1892)—Chacalluta (Arica) in extreme northern Chile along the coasts and lower-lying valleys north to Trujillo, Peru (Fjeldså and Krabbe 1990, Johnson 1967).

brachyptera (Richmond 1896)—Margarita Island off north coast of Venezuela and parts of mainland. Kelso (1934) listed this as the short-winged burrowing owl, which is, of course, a redundancy, with its racial designation. The data in Table 1 support that designation.

tolimae (Stone 1899)—western Columbia.

juninensis (Berlepsch and Stolzmann 1902)—The puna of the Andes from Jujuy in northwestern Argentina through southwestern Bolivia (Lake Poopó) to the departments of Junín and Lima in central Peru (Fjeldså and Krabbe 1990, Johnson 1967). Koepcke (1970) listed the smaller *nanodes* on the Peruvian coast and low Andean slopes and this larger race in the puna.

Table 2. Distribution of former and present insular races of the burrowing owl.

ISLAND GROUP/ISLAND-LOCALE	RACE	SOURCE	EVIDENCE
Bahamas			
Grand Bahama	*floridana*	Barbour (1943)	live birds
Great Abaco	*floridana*	Olson & Hilgartner (1982)	fossil
New Providence	*floridana*	(Ridgway 1914, Olson & Hilgartner 1982)	skins
Andros	*floridana*	Ridgway (1914)	skins
Eleuthera	*floridana*	(Ridgway 1914, Olson & Hilgartner 1982)	fossil
Little Exuma	*floridana*	(Ridgway 1914, Olson & Hilgartner 1982)	bones
Great Exuma	*floridana*	(Bangs 1930, Olson & Hilgartner 1982)	skins
Crooked Island	*floridana*	(Ridgway 1914, Olson & Hilgartner 1982)	skins
Great Inagua	*floridana*	(Ridgway 1914, Olson & Hilgartner 1982)	skins
Samana Cay	*floridana*	(Ridgway 1914, Olson & Hilgartner 1982)	skins
Cay Sal	*floridana*	Ridgway (1914)	skins
Greater Antilles			
Cuba—Pinar del Río	*floridana*	Olson & Hilgartner (1982)	live birds
—Metanzas	*floridana*?	Olson & Hilgartner (1982)	fossil
—near Guantánamo	*floridana*[a]?	Olson & Hilgartner (1982)	fossil
—Cayos Coco	*floridana*?	Olson & Hilgartner (1982)	
—Guillermo	*floridana*?	Olson & Hilgartner (1982)	fossil
—Daiquirí	*floridana*?	Olson & Hilgartner (1982)	fossil
—Campo Florido, Havana	*floridana*	Bond (1943)	skins
Cayman Brac (extirpated)	*floridana*?	(Olson & Hilgartner 1982, Pregill et al. 1988)	fossil
Jamaica (extirpated)	*floridana*?	(Olson & Hilgartner 1982, Pregill et al. 1988)	fossil
Hispaniola			
Haiti—Le Coup	*troglodytes*[b]	Ridgway (1914)	skins
—Port au Prince	*troglodytes*[b]	Ridgway (1914)	skins
—near Lake Gautier	*troglodytes*[b]	Ridgway (1914)	skins
Dominican Republic—Azua	*troglodytes*[b]	Ridgway (1914)	skins
—between La Vega and Domingo City	*troglodytes*[b]		
—12 km ne of Jarabacoa	*troglodytes*	LSU–Baton Rouge collection	skins
—Gonâve Island	*troglodytes*	Wiley (1986[a])	
—Beata Island		(Olson & Hilgartner 1982, Wiley 1986[a])	fossil
Mona Island (extirpated)		(Olson & Hilgartner 1982, Pregill et al. 1988)	fossil
Puerto Rico	[c]	(Olson & Hilgartner 1982, Wiley 1986[b])	fossil
Lesser Antilles			
Bermuda (extirpated)	*amaura*	(Olson & Hilgartner 1982, Pregill et al. 1988)	fossil
St. Kitts (extinct)	*amaura*	(Wing et al. 1968, Olson & Hilgartner 1982, Pregill et al. 1988)	fossil
Nevis (extinct)	*amaura*		
Antigua (extinct)	*amaura*	(Wing et al. 1968, Olson & Hilgartner 1982, Pregill et al. 1988)	skins
		(Cory 1891, Ridgway 1914, Deignan 1961, Wing et al. 1968, Olson & Hilgartner 1982, Pregill et al. 1988)	skins
Guadeloupe	*guadeloupensis*	Bangs (1930)	skins
Marie-Galante	*guadeloupensis*	(Deignan 1961, AOU 1983)	skins
Redonda	?	Deignan (1961)	skins
Margarita—Porlamar	*brachyptera*	(Deignan 1961, Meyer de Schauensee & Phelps 1978)	skins
La Borracha	*brachyptera*		
Cubagua	*brachyptera*	Meyer de Schauensee & Phelps (1978)	
		Meyer de Schauensee & Phelps (1978)	

Table 2. Continued.

ISLAND GROUP/ISLAND-LOCALE	RACE	SOURCE	EVIDENCE
Revillagigedo group			
Mexico—Pacific Ocean			
Clarion Island	*rostrata*	(Ridgway 1914, Deignan 1961)	skins
Netherlands Antilles			
Aruba	*arubensis*	Cory (1915)	skins

[a] May represent an, as yet, unnamed subspecies (Olson & Hilgartner 1982).
[b] Presumed to be of this race.
[c] Possibly a new species? See Olson & Hilgartner (1982).
[d] When no evidence is offered none is indicated on the table.

punensis (Chapman 1914)—Semiarid valleys of northern Peru to the lowlands of western Ecuador (Fjeldså and Krabbe 1990).
arubensis (Cory 1915)—Aruba Island off northern coast of Venezuela.
intermedia (Cory 1915)—Coast of Peru from south of Payta to Pacasmayo (Peters 1940).
minor (Cory 1918)—Savannas of the upper Rio Branco (Brazil) and probably adjacent parts of British Guiana (Snyder 1966) and Surinam.
carrikeri (Stone 1922)—Known only from type locality (Palmar, Boyaca) in the eastern Andes of Colombia.
pichinchae (Boetticher 1929)—Western Ecuador north to Quito.
boliviana (Kelso 1939)—Arid habitats in tropical Bolivia and northern Argentina.
apurensis (Gilliard 1940)—Northcentral Venezuela.
partridgei (Olrog 1976)—Northwestern Argentina.

DISCUSSION

Although every attempt has been made to include the material from all pertinent literature, much of the distribution of the burrowing owl is within South America and the Caribbean region and the literature is in journals that are not always widely available. It has been the intent of the author to be as inclusive as possible with the literature and to identify those geographic and taxonomic regions where much more work is needed. Olson and Hilgartner (1982) recognized the need to reevaluate the birds from Cuba as there are two races represented there or perhaps a new race. The populations of some of the Caribbean Islands also appear to warrant investigation and one wonders about the possibility of reintroducing the most similar race to those islands where it has been extirpated or where entire races have been eliminated. It is for the convenience of those familiar with those regions or for those who may be traveling to those areas that Table 2 and Figure 2 have been presented. From the anatomical data (Table 1) some trends can be observed; e.g., the continental populations tend to be larger than the insular races. This is particularly true with regard to the tarsal measurements with *rostrata* being something of an exception. It should also be noted that some of the sample sizes are much smaller than desired but, because that is all there is, they are summarized here. While much more information is needed, it should be obtained from live trapped birds, be carefully documented photographically and then the birds should be released back into the wild. Also much needs to be learned about the behavior of the species over much more of its range. It was particularly perplexing trying to work out the distributional range of the various races in South America and it is obvious to me that there is a challenge awaiting some student to assemble the available information from museum specimens. Rocha (1990) could serve as a model for such studies. Also it would be useful to carefully examine, or reexamine in some cases, specimens so that a more accurate picture of the races can emerge. The work that has been and is being done with the species at the limits of its range (e.g., Saskatchewan and Manitoba) and where it is under pressures from anthropogenic development should be extended to the species in the Caribbean and many parts of South America. There seems to be considerable information, with regard to the study of the species, and there seems to be much pertinent information becoming available, or applicable to, the management of the species in areas of high owl-human interaction. Much of this information is available in English but it is needed in Spanish. The inclusion of abstracts and figure and table captions in Spanish, of all articles on the species would be a useful addition where not presently available. Also the careful examination of what is available and the translation of key material into a species management handbook would also seem a useful approach for the conservation of the species. Because of its inhabiting more arid areas, the burrowing owl has been able to stay out of conflict situations in some regions, but as the ever-increasing human population increases its demands for more irrigation-based food, owl-human interaction should be expected to increase in the future and obviously, not in favor of the burrowing owl.

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POPULATION AND ECOLOGY AND STATUS

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USING THE AREA OCCUPIED METHOD TO SURVEY FOR BURROWING OWLS IN SOUTH DAKOTA

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Abstract.—Using point-transect survey methods and area occupied analysis we developed a census technique for burrowing owls (*Speotyto cunicularia*) in Badlands National Park, South Dakota. During June and July of 1991, transects were established on four prairie dog towns within the park. We visited stations spaced 300 m apart along the transect for 10 minutes and looked and listened for owls. Surveys were repeated an average of six times on the two towns on which we found owls in 1991, and were also carried out on 11 other towns in the park. Data were analyzed using the area occupied method. We located 12 broods with 29 young, and 31 broods with 99 young in 1991 and 1992, respectively. We estimated the proportion of the area surveyed which was occupied by owls to be 0.34 (SE = 0.07) in 1991 and 0.57 (SE = 0.07) in 1992. The probability of detecting an owl at any occupied station was approximately 0.49. We were able to establish a census technique for Badlands National Park that can be carried out by Park biologists with a minimum of training. Results can be compared among years to form a framework for managing burrowing owls in the Park. We believe that this technique has application to other areas where burrowing owls nest in semi-colonial situations.

Key Words: Speotyto cunicularia; *burrowing owl; South Dakota; survey technique; management.*

Utilizacion del metodo de area ocupada para muestrear tecolotitos enanos en South Dakota

Resumen.—Utilizando los metodos de muetreo de transectos de conteos de punto y area ocupada desarrollamos una tecnica de censar para el tecolotito enano (*Speotyto cunicularia*) en Badland National Park, South Dakota. Durante junio y julio de 1991 transectos se establecieron en 4 colonias de perritos de la pradera dentro del parque. Visitamos estaciones separados por 300 m a lo largo de transectos durante 10 minutos y observamos y escuchamos a tecolotes. Censos se repitieron un promedio de 6 veces en dos colonias en las cuales encontramos tecolotes en 1991 y se llevaron a cabo en otras 11 colonias dentro del parque. Los datos se analizaron usando el metodo de area ocupada. Localizamos 12 nidadas con 29 pollos y 31 nidadas con 99 pollos en 1991 y 1992, respectivamente. Estimamos que la proporcion del area censada que estaba ocupada por los tecolotes era de 0.34 (se = 0.07) en 1991 y 0.57 (se = 0.07) en 1992. La probabilidad de detectar un tecolote en una estacion ocupada era de aproximadamente 0.49. Pudimos establecer una tecnica de muestreo para Badlands National Park que puede realizarse por biologos del parque con un minimo de entrenamiento. Los resultados pueden compararse entre años para formar una base para el manejo del tecolotito enano en el parque. Creemos que esta tecnica tiene aplicacion en otras areas donde los tecolotes anidan en situaciones semi-coloniales.

[Traducción de Filepe Chavez-Ramirez]

Introduction

Accurate survey methods are needed for successful management, research, and conservation of wildlife populations. Many methods have been used to survey raptor populations, including road transect counts, aerial counts, nest searches, and call-playback techniques (Fuller and Mosher 1987). A method to efficiently and accurately survey breeding burrowing owls (*Speotyto cunicularia*) has previously not been available to wildlife managers.

Typically, population data on burrowing owls have fallen into one of three categories: (1) estimates of status at the state or provincial level, usually gathered through questionnaires or "best guesses" (Wedgwood 1976, Martell 1990); (2) searches using call-playback or road transect survey methods (Martell et al. 1990); or (3) in local areas, intensive searches sometimes burrow by burrow, often conducted during the course of a basic research project (MacCracken et al. 1985).

Although intensive searches can lead to finding most owls on a local area, they are time consuming, hard to repeat, and expensive, making them of little use for long-term monitoring or management purposes. Furthermore, burrowing owls are difficult to accurately survey because, like other raptors, they are wide-ranging, secretive, and occur at relatively low densities compared to most game animals (Iverson and Fuller 1989).

This lack of repeatable, economical survey techniques led us to work with the National Park Service to develop a census technique for burrowing owls in Badlands National Park. Our objective was to develop an accurate, repeatable, method for monitoring the Park's burrowing owl population, which in future years could be implemented using Park personnel within the framework of a limited research and management budget.

STUDY AREA

This study was conducted in Badlands National Park which covers 98 865 ha and is located in western South Dakota, approximately 113 km east of Rapid City, SD. It is an area of rugged geological formations including steep "walls" surrounding short-grass plains. These plains consist primarily of western wheatgrass (*Agropyron smithii*), *Bromus* spp., blue grama (*Bouteloua gracilis*), and threadleaf sedge (*Carex filifolia*). Colonies of black-tailed prairie dogs (*Cynomys ludovicianus*) create "towns" covered by buffalo grass (*Buchloe dactyloides*) and needle-and-thread grass (*Stipa comata*) (Agnew et al. 1986), providing ideal habitat for burrowing owls. A herd of nearly 500 American bison (*Bison bison*) also graze the plains in the western portions of the Park.

METHODS

To develop and test the census method, four prairie dog towns (Burns, Tyree I, Roberts, and Sage) with a total area of 760 ha (Table 1) were surveyed six times between 15 June and 15 July 1991. Surveys were repeated on Burns and Tyree I in 1992, but not on Roberts and Sage because of an absence of owls in 1991. Towns were chosen because their size, past management history, and future management plans made them representative of towns in the Park. To obtain an estimate of the Park's burrowing owl population, 13 towns totaling 1506 ha were surveyed at least once in 1992.

We established straight line transects with stations 300 m apart through the prairie dog towns (Ralph and Scott 1981). On smaller towns, transect lines were established through the center of the town. On larger towns, transects were established 300 m apart and parallel to each other allowing for maximum coverage of the area.

Table 1. Burrowing owl brood counts in Badlands National Park 1991–92.

PRAIRIE DOG COLONY	HA.	BROODS 1991	BROODS 1992	JUVENILES 1991	JUVENILES 1992
Burns	204	1	4	2	21
Tyree I	118	5	5	9	16
Tyree II	39	2	1	6	3
Roberts	130	0	1	0	3
Sage	308	0	0	0	0
Kocher I	327	4	9	12	19
Other	380	0	11	0	37
Total	1506	12	31	29	99

The presence of prickly pear cactus (*Opuntia* spp.) and other low-lying vegetation, combined with the owls' cryptic coloration, presented problems in locating owls. Using visual field tests, we determined that a reasonable scanning distance of 150 m from the observation point would allow most Park biologists to reliably locate and identify owls at their burrows.

Each station was visited for 10 min. Using binoculars and 15–60× spotting scopes, we searched for owls within the 150 m radius. In order to maintain consistency and maximize the probability of sighting resident owls, surveys were always done from dawn until approximately 1000 hrs and again from 1900 hrs until 2200 hrs, or until visibility was impaired by darkness. Surveys were not done during inclement weather.

The relatively low densities of owls found on each survey made the use of standard statistical analysis associated with point-transect methods inappropriate. This prompted us to use the "area occupied method" (AO) developed by Geissler and Fuller (1986). Originally developed for censusing diurnal woodland raptors (Iverson and Fuller 1989), the AO technique estimates the proportion of an area which is occupied by a species, thus providing an index of the species abundance.

We also determined the "probability of detecting" (PD) burrowing owls at an "occupied" station. The PD was derived from the repetition of surveys, yielding an arithmatic mean of dl, which is the proportion of detections occurring after the first detection at each stop (Iverson and Fuller 1989). The PD is used as a correction factor for the AO, and can help in future survey design by indicating how many times a transect line should be walked to ensure adequate coverage.

To determine the AO, we recorded whether an adult owl was detected at each station on the transect (i.e., within the 150 m radius). The number of stations on a town that were occupied by adult owls was divided by the total number of stations, then multiplied by the PD correction factor. The resulting statistic gave the proportion of the area which was occupied by owls, along with esti-

Table 2. Probability of detection and area occupied by burrowing owls in Badlands National Park 1991–92.

	Probability of Detection				Area Occupied			
	Mean	SE	95% CI	N	Mean	SE	95% CI	N
1991	0.448	0.097	0.247–0.663	48	0.340	0.070	0.186–0.499	75
1992	0.564	0.068	0.428–0.700	75	0.570	0.072	0.439–0.723	129
2 yr	0.486	0.056	0.376–0.598	123	—	—	—	

mated SE and 95% Confidence Intervals (CI). Geissler and Fuller (1986) present a detailed explanation of AO and PD along with the equations necessary for computation.

Results

In 1991 we located 12 broods and counted 29 young during our surveys, while in 1992, sampling a much larger area of the Park, we located 31 broods and counted 99 young (Table 1). We estimated that owls occupied 34% (SE = 0.07) of the area occupied by prairie dog towns in the Park in 1991 (N = 75 stations, 95% CI between 0.19–0.5) and 57% (SE = 0.07) of the towns in 1992 (N = 129, 95% CI between 0.44–0.72) (Table 2). In 1991, using data from four prairie dog towns (N = 48 stations), we determined the PD was 0.45 (SE = 0.1), with a 95% CI of 0.247–0.663. When we combined this with the data from Tyree and Burns sites in 1992 (total N = 75 stations), we obtained a PD of 0.486 (SE 0.056) and reduced the 95% CI to 0.376–0.598 (Table 2).

Discussion

We located more owls in the Park in 1992 than in 1991. This is partially due to having increased the area surveyed in 1992 (from 760 to 1506 ha). The increased number of broods on three of six towns in 1992 (Table 1), combined with an increase in the AO from 0.34 to 0.57 (Table 2), indicates a real increase in owl numbers.

The probability of detecting a burrowing owl on our study area was relatively good at 0.49. This compares with an average PD of 0.34 for red-shouldered hawks (*Buteo lineatus*) in Indiana (Iverson and Fuller 1989). Some variation in PD is to be expected with the variations in habitat and owl behavior. However, the PD on individual towns was fairly consistent ranging from 0.33 on Roberts in 1992 (only one station having a sighting) to 0.71 on Tyree in 1992.

We believe that visually counting burrowing owls on a walking point-transect survey is an appropriate census technique for Badlands National Park. It is a relatively simple and inexpensive method which can be carried out in the future by Park biologists with a minimum of training. Using the area occupied method of analysis will allow Park managers to monitor the long-term stability of owl populations and form a framework for future management. Park biologists will also be able to assess the effects on burrowing owls of management actions taken in the Park. This may include such activities as black-footed ferret (*Mustela nigripes*) reintroduction or changes in prairie dog control programs. This technique can be applied to other areas where burrowing owls nest in semicolonial situations, especially where the species is not considered endangered but monitoring is desired. It must be remembered that this technique provides an index, not an actual count, of owls (Iverson and Fuller 1989). Thus, for areas where there are serious concerns about an endangered owl population, more intensive surveys combined with population data are certainly needed.

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DEMOGRAPHY AND POPULATION DYNAMICS OF THE BURROWING OWL

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ABSTRACT.—I used deterministic, age-structured analytic models to examine the demographic causes of projected and observed declines in the size of a color-marked burrowing owl (*Speotyto cunicularia*) population, and to predict its persistence time. Estimates of burrowing owl demographic parameters were calculated from direct observations and from genetic analyses of reproductive success. Comparison of theoretical expectations (based on actual demographic traits) with the real dynamics of the population over ten years showed that the population declined to reproductive extinction in half the time predicted by the models. This discrepancy suggests that stochastic variation in demographic traits, possibly caused by weather, along with stochastic and deterministic changes in genetic structure, also contribute to the dynamics and persistence of burrowing owl populations.

KEY WORDS: *Burrowing owls;* Speotyto cunicularia; *demography; population dynamics; population modeling.*

Demografia y dinamica de poblacion del tecolotito enano

RESUMEN.—Use modelos deterministicos de estructura de edades para examinar las causas demograficas de disminucion proyectadas y observadas en el tamaño de una pobalcion marcada del tecolotito enano con fines de predecir su tiempo de persistencia. Estimaciones de parametros demograficos del tecolotito se calcularon de observaciones directas y de analisis genetico del exito reproductivo. Comparaciones de expectativas theoricas (en base a rasgos demograficos reales) con la dinamica de la poblacion atravez de 10 años mostro que la poblacion disminuyo a extincion reproductiva en la mitad del tiempo predicho por los modelos. Esta discrepancia sugiere que variaciones fortuitas en rasgos demograficos, posiblemente el clima, ademas de cambios al azar y deterministicos en la estructura genetica tambien contribuyen a la dinamica y persistencia de poblaciones del tecolotito enano.

[Traducción de Filepe Chavez-Ramirez]

The dynamics of populations are collectively governed by demographic traits (such as birth and death rates), population size, degree of spatial subdivision, and levels of immigration and emigration. As natural populations become smaller and more subdivided due to human activities, population ecologists have focused their attention on how variation in demographic parameters, population size, and spatial structure interactively affect population dynamics, and especially the prospects for species extinction or persistence (Gilpin and Soulé 1986, Goodman 1987a,b, Shaffer 1987, Lande 1988, Simberloff 1988). Population viability analysis seeks to identify those demographic components of a species' life history that most substantially affect long-term persistence. Such analyses generally employ deterministic mathematical models to predict the state of a population at some time in the future, given a set of age- or stage-specific demographic parameters. In general, studies using these methods suggest that even small differences in demographic traits, spatial structure, population size, and levels of dispersal can individually and collectively have a large effect on probabilities of persistence or extinction.

The burrowing owl is widely distributed through arid regions of the western hemisphere, where it usually inhabits burrows initially excavated by fossorial mammals (particularly rodents) or reptiles (Zarn 1974). At one time, the burrowing owl was apparently locally abundant over much of its range, but at least in western North America (and perhaps throughout its geographic distribution), it has substantially declined in numbers since the early 1900s (see Bent 1938, Arbib 1979). In Cali-

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fornia, the burrowing owl was reported to have been common at the turn of the century (Grinnell and Miller 1944). Since then, as its preferred habitat of short grassland has been usurped and fragmented by human development, and as rangeland managers have extensively used rodenticides, burrowing owl numbers have declined, while the distances between populations have increased (unpublished data).

All of these demographic and habitat attributes suggest that the burrowing owl may be particularly sensitive to extinction. Nonetheless, without quantitative information about the demographic traits of burrowing owl populations, it is unclear whether this species will persist locally, and if so, for how long. To begin to answer these questions, I began a demographic, behavioral, and genetic study of a population of burrowing owls in Davis, California, in 1985. Because burrowing owls in my study area had been censused since 1981, I was able to estimate demographic parameters and compare theoretical expectations to the actual trend in population size during a ten-year period.

METHODS

Study Area and Population Size. I studied a population of wild burrowing owls occupying 150 ha of mostly nonnative annual grassland on the campus of the University of California, Davis, California. The owls roosted and nested in burrows excavated by California ground squirrels (*Spermophilus beecheyi*), and they were somewhat habituated to humans, a characteristic that facilitated their study. The grassland tracts were mowed several times during spring and summer for fire control and to improve visibility of the owls with binoculars and spotting scopes.

Changes in the size of this burrowing owl population were measured each year from 1981 through 1991. The total number of territories occupied in each year was determined by spot-mapping (International Bird Census Committee 1970). In 1981–84, T. Schulz of the UC Davis Raptor Center conducted diurnal censuses of adult owls during the breeding season. In 1985–91, I censused adults and juveniles during the reproductive periods and made incidental surveys during some winters.

Burrowing Owl Life History. Like other owls, burrowing owls breed once per year in an extended reproductive period, during which most adults form monogamous pairbonds. However, occasional polygamy and extra-pair fertilizations confound the determination of parentage from field observations (see Johnson 1996b). For estimates of individual reproductive success I therefore incorporated two years of data on genetic parentage, as determined by DNA fingerprinting.

In field studies of burrowing owls during the breeding season, three developmental stages can be identified and monitored: (1) emergent nestlings (up to 3–4 wk old), (2) juveniles, including both fledglings and independent preadults (through age 14–15 wk), and (3) adults. When developing nestlings first emerge from the burrow, they are covered with gray natal down, and they remain near the burrow entrance. A week later, the full-grown nestlings will have molted into a distinctive juvenile plumage in which their heads and backs are solid brown and their breasts and undercoverts are plain beige with no bars. At this time the young owls also begin to fly, becoming competent fliers within 2–3 wk of emergence. Fledgling burrowing owls could be easily identified as such by their plumage until September, by which time they had molted into a cryptic plumage of barred light brown feathers, making them indistinguishable from adults.

Color-Banding and Censusing. I color-banded 112 wild burrowing owls (25 as adults, 87 as juveniles) in 1985–88 during the fledging period (late June through July). Owls were captured with noose carpets and one-way-door traps. Every bird was fitted with a unique combination of 3 colored nylon bands and 1 aluminum U.S. Fish and Wildlife Service band (2 bands per leg). I used a stationary vehicle as a blind and made behavioral observation with binoculars and a spotting scope from distances of between 50–200 m. From direct observations and censuses of all banded and unbanded individuals at least once every two days, I was able to estimate survival rates for juveniles and adults, in addition to individual-specific fecundity for adults of both sexes. Individual reproductive success in 1987–88 was further estimated using DNA fingerprints from 67 of the wild color-banded owls (see Johnson 1996b).

RESULTS

Estimates of Demographic Parameters. I estimated juvenile (s_0) and adult (s) survivorship in three ways, based on data in Table 1, which tracks the survival of unbanded nestlings, juveniles, and adults, in addition to color-banded juveniles and adults, during 1985–89. The survival estimates, denoted "worst case," "intermediate," and "best case," respectively, reflect three increasingly optimistic assumptions: (1) the proportion of the color-banded sample that is known to have survived to the next year accurately represented survival in the population at large, (2) emigration equaled immigration, therefore the number of Davis owls that could have dispersed and survived equaled the number of unbanded adults (putative immigrants) that appeared in the Davis population the next year, or (3) all of the Davis owls that disappeared actually dispersed to survive elsewhere. Estimates based on (1) represent minimum estimates, and they may be the most reliable, especially if the population is closed to emigration and immigration. Estimates that assume (2) are certainly possible, but it is also plausible that unbanded owls were already population members. By this method, population growth was likely overestimated because the survival rate used for each age class assumed

Table 1. Burrowing owl demographic data, 1985–88.

	1985	1986	1987	1988
No. territories	11	12	11	9
No. adults	21[a](7)[b]	23(12)	24(22)	18(16)
Died	0	0	2–5[c](1)	1(1)
Disappeared	18(4)	18(3)	9–12[c](3)	10–12[d](8)
Remain in yr_{t+1}	3(3)	5(5)	10(10)	5–7[d](5–7)[d]
No. emerged nestlings	28(17)	39(21)	24(18)	37(31)
Died (nestlings)	2	2	3	6
Died (juveniles)	2(2)	4(2)	0–3[c](0)	1(1)
Disappeared	20(11)	28(14)	15–18[c](15)	22(22)
Remain in yr_{t+1}	4(4)	5(5)	3(3)	8(8)
No. unbanded adults in $year_{t+1}$	11	2	2	2–4[d]
No. nestlings/adult	1.33	1.70	1.00	2.06
No. successful adults[e]	12	18	15	17
No. nestlings per successful adult	2.33	2.17	1.60	2.06

[a] Includes both color-banded and nonbanded burrowing owls.
[b] Color-banded owls only.
[c] Three unbanded owls that could not be assigned to an age class died in winter 1987. I made one estimate of survivorship as if they had all been adults, and another as if they had all been juveniles.
[d] The discrepancy between the two values is due to two disputable color-band sightings in 1989.
[e] An adult was considered to have successfully reproduced if nestlings emerged from its burrow. Success of 18 owls in 1987–88 was further verified by DNA fingerprinting (see Johnson 1996a).

that all putative immigrants were either juveniles or adults, respectively, in the previous year, rather than a combination of the two. Estimates that assume (3), are extremely optimistic and unlikely; I include them only to define the maximum possible value of reproductive output.

Depending on which assumption they were based, estimates of the probability of juvenile burrowing owl survival, which is equal to the chance of surviving to age at first breeding (1 yr), were 0.23 (worst case), 0.35, or 0.93 (best case). Annual adult survivorship was estimated to be 0.42 (worst), 0.54, or 0.93 (best). I used each set of adult and juvenile survival rates to independently project three different population growth rates, while holding fecundity and age at first reproduction constant.

For the fecundity parameter I estimated the mean *per capita* rate of reproduction, $b = 1.49$ (± 1.251 SD; $N = 86$), by dividing the number of newly emerged nestlings in 1985–88 by the total number of adults present in those years. I estimated that each pair of owls produced from 0–9 nestlings (0–4.5 offspring per individual). Onset of reproduction in both sexes occurs when owls are one year old and the burrowing owl life cycle is characterized by birth-pulse reproduction (Caughley 1977, Caswell 1989), with an interbirth interval of one year, making it appropriate for modeling in discrete time (Cole 1954).

Projected Population Growth Rate. Using the sets of demographic parameters described above, I determined the theoretical finite rate of growth for the Davis burrowing owl population by solving the Euler-Lotka equation, $1 = \Sigma \lambda^{-x} l_x b_x$, for λ. In this equation, l_x is the probability of surviving to age x, and b_x is age-specific fecundity.

Projected population growth rates calculated from the three increasingly optimistic sets of burrowing owl survival rates were 0.8319, 1.0410, and 1.7307. Demonstrable survival rates of banded juveniles and adults produced a value for λ (0.8319) that was much lower than 1.0, indicating a population declining by almost 17% per year. By contrast, the values for λ that were derived from the "intermediate" and "best case" survivorships signify populations increasing by 4% and 73% per year, respectively.

Expected Persistence Time. I calculated the time, in years subsequent to 1981, that the Davis burrowing owl population with an initial size of 44 adults could have been expected to persist if it ex-

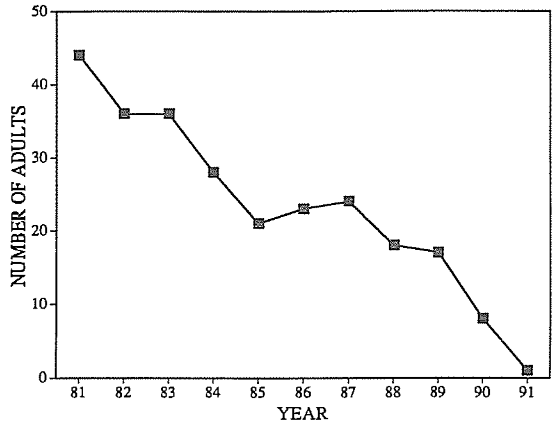

Figure 1. Observed rate of change in numbers of burrowing owls in the Davis population from 1981–91. The number of adults declined from 44 to 1 over the 10-year period.

Table 2. Actual sizes and annual growth rates of the Davis burrowing owl population, 1981–91.

YEAR	NUMBER OF ADULTS	ANNUAL RATE OF GROWTH (λ)
1981	44	—
1982	36	0.8182
1983	36	1.0000
1984	28	0.7778
1985	21	0.7500
1986	23	1.0952
1987	24	1.0435
1988	18	0.7500
1989	17	0.9444
1990	8	0.4706
1991	1	0.1250

perienced a sustained negative rate of change of 0.8319, as analysis with parameters estimated from the sample of color-banded burrowing owls implies it was. Using the formula $T_{extinction} = -\log N/\log \lambda$ (Lande 1985), persistence time for this population was expected to be 20.6 yr.

Observed Population Decline. The actual growth rate for this burrowing owl population was computed directly from the observed population trajectory over the 10-year interval 1981–91. The actual population trend is portrayed graphically in Fig. 1. Total population size (number of adults) in each year and annual growth rates are given in Table 2. I empirically obtained λ, which is equal to the geometric mean of the yearly changes in size, each of which was computed from N_t/N_{t-1}. The actual rate of population change was 0.6849, equivalent to a sustained 31.5% decline since 1981.

DISCUSSION

By using a deterministic approach, I was able to predict the likelihood that the Davis burrowing owl population would become extinct, and over what time scale. The results of this analysis show that the owl population actually declined to extinction in half the time predicted by my most reliable estimates of demographic parameters for owls in 1985–88. However, deterministic analyses assume conditions which are often not upheld by biological populations (i.e., constant vital rates, stable age distribution, closed population). Therefore, some imprecision with this modeling approach is to be expected. In reality, the demographic traits, and consequently the dynamics, of this wild population, and probably most others, can vary in a complex manner.

As shown for the Davis burrowing owls, forces other than systematic ones undoubtedly influenced population dynamics over the 10-year period, to produce a rate of decline 1.88 times that predicted (31.5% compared to 16.8%). Although I used average demographic parameters in my analysis, I observed substantial year-to-year variation in survivorship, with mean annual survival of juveniles varying by 35%, and that of adults by 50%. Similarly, adult fecundity varied among years and between sexes by a factor of two. No conspicuous trends were revealed in either parameter, and the demographic significance to the burrowing owl of such variation in vital rates is not known. However, in keeping with small population theory (Goodman 1987b), if the role of chance demographic events increases with decreasing population size, demographic stochasticity should have been particularly important for an already small population in the last phase of decline.

Other nondeterministic factors could have been important. Two catastrophic climatic events, a drought in 1987–91 and an extended winter freeze in 1990–91, also may have affected vital rates in those years, by causing mass mortality or forcing nomadic dispersal. Drought, in particular, is known to affect the population dynamics of other insectivorous vertebrates (Lack 1968). Due to lack of specific field evidence, however, the importance of these factors to the Davis burrowing owl population remains unclear.

My analysis of burrowing owl population persistence was further limited because it was done out of context of the regional population. Theoretical predictions suggest that larger size should buffer subpopulations against extinction from most stochastic events, whereas regional persistence is enhanced by high numbers of independent subpopulations occupying habitat patches that are separated enough to spread environmental and disease risk, yet close enough to ensure recolonization (Gilpin and Soulé 1986). In any case, dispersal among local populations regulates regional dynamics; unfortunately, it is also one of the most difficult parameters to estimate for wild populations, especially for nocturnal owls.

Little is known about dispersal in the burrowing owl. California populations are primarily resident, with adults and juveniles exhibiting local site fidelity. Root mean square dispersal distances were 0.2 km for adults and 0.5 km for juvenile owls in the Davis population. Based on the sample of color-banded burrowing owls, a very small number of juveniles (2 of 87) dispersed from the study area. However, such movements probably did not result in successful colonization. One juvenile burrowing owl dispersed 1.5 km from its natal burrow to a winter roost under a temporary building at a construction site; it disappeared within 2 wk. The other juvenile dispersed 12 km to landscaped grounds of a residential complex, where it resided in a cement culvert for more than 1 yr, at which time it was still without a mate. Systematic searches of appropriate habitat within 15 km of the Davis population in 1986–89 found none of the color-banded owls that had disappeared from the study area. However, other North American burrowing owl populations are seasonally migratory, with owls flying hundreds of kilometers in winter (Zarn 1974). Some of the Davis burrowing owls may have dispersed long distances, but none of the 80 color-banded owls that disappeared from the Davis population were reported to have been recovered at distant locations.

A further complication in the analysis of population viability is that the dynamics of natural populations are controlled by an interplay between ecological and genetic processes. The methods of viable population analysis used to predict population peristence in this study, and virtually all others, generally do not incorporate the population genetic effects of changing demographies. Importantly, the same ecological processes that directly drive population decline may indirectly exacerbate the likelihood of extinction by inducing changes in the genetic structure of a species. My genetic data suggest that the Davis burrowing owl population is inbred with respect to a hypothetical panmictic population (see Johnson 1996a), but how this might have affected the persistence of my study population, and whether other burrowing owl populations are comparably inbred, remains to be seen. Other studies on spatially-structured populations present equivocal results on the fitness consequences of inbreeding, and as with attempts to assess the effects of genetic variation on fitness, no firm conclusions can be drawn.

As shown by this investigation of burrowing owl dynamics, many processes likely affect population persistence at once. A more comprehensive and robust theory of population dynamics for this species will therefore require a synthesis of the effects of both demographic and genetic processes in a stochastic spatially-structured framework.

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J. Raptor Res. Report 9:34–37

PARAMETERS OF A DECLINING BURROWING OWL POPULATION IN SASKATCHEWAN

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ABSTRACT.—A declining population of banded burrowing owls was studied in Saskatchewan from 1986–92. Annual adult survival increased significantly over the period of study. However, the proportion of pairs that produced young, and the number of chicks produced per nest attempt declined, the former significantly so. In no year was productivity sufficient to offset adult mortality. A simple model predicted the decline of the study population. Despite decreasing over the period of study, the adult mortality rate appeared to be too high, based on body weight and other studies of stable populations. This was exacerbated in some years by poor reproductive success. Juvenile mortality appeared to be normal. The cause of the decline is not known, but excessive predation facilitated by the heavily fragmented habitat is suspected. Other factors may also be operating on the still unknown wintering grounds.

KEY WORDS: *burrowing owl*; Speotyto cunicularia; *status*; *Saskatchewan*; *reproduction*; *mortality*; *Canada*.

Parametros de una poblacion de tecolotito enano en disminucion en Saskatchewan

RESUMEN.—Una poblacion en disminucion de tecolotitos enanos anillados se estudio en Saskatchewan de 1986 a 1992. Sobrevivencia anual de adults aumento significativmente durante el periodo de estudio. Sin embargo la proporcion de parejas que produjeron crias y el numero de pollos producidos por nidada disminuyo, el primero significativamente. En ningun año fue suficiente la productividad para remplazar la mortalidad de adultos. Un modelo sencillo predice la disminucion de la poblacion bajo estudio. A pesar de que la mortalidad de adults disminuyo durante el periodo de estudio, la tasa de mortalidad de adultos parece ser demasiado alta basada en peso y otros estudios de poblaciones estables. Esto se agrava en algunos años de baja reproduccion. La mortalidad de juveniles aparenta ser normal. La causa de la disminucion no se conoce, pero depredacion excesiva facilitada por la gran fragmentacion del habitat se sospecha. Otros factores pueden estar operando en las areas invernantes aun desconocidas.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) is designated as Threatened in Canada by the Committee on the Status of Endangered Wildlife in Canada (Wedgwood 1978, Haug and Didiuk 1991). This means that it is likely to become an endangered species unless the limiting factors operating against it are reversed. Several such factors have been identified (Wedgwood 1978). In 1986, a study was initiated in Saskatchewan to evaluate them in a systematic fashion. To date, studies have been conducted on grasshopper insecticides (James and Fox 1987, Fox et al. 1989, Fox and James 1991), rodenticides (James et al. 1990), and habitat (James et al. 1991, James 1993). We report here on the population dynamics of this study population.

STUDY AREA AND METHODS

The study was conducted on the Regina Plain south of the City of Regina, Saskatchewan (50°27'N, 104°37'W) from 1986–92. The area is mostly devoted to the production of wheat and other crops. The burrowing owls nest on the few remaining highly fragmented and dispersed pastures. Each year, all owl pairs were located, their reproductive success monitored, and as many adults and chicks as possible were captured and banded. Each nesting pair was counted as one nest attempt, and a nest attempt was counted as successful if at least one chick was fledged.

We derived and used the following formula to calculate annual adult survival rates:

$$S_a = [R_t + R_t/C_t(A_t - C_t)]/B_{t-1}$$

where S_a = survival rate of adults, R_t = no. banded adults recaptured in year t, B_{t-1} = no. adults banded in year

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Table 1. Reproductive success of burrowing owls on the Regina Plain, Saskatchewan.

YEAR	NO. NESTS	% SUCCESSFUL[a]	NO. CHICKS/ SUCCESSFUL NEST	NO. CHICKS/ NEST ATTEMPT
1986	99[b]	72	4.3	3.1
1987	221[b]	75	5.3	4.0
1988	55[b]	85	5.3	4.5
1989	54[b]	57	2.9	1.7
1990	39	49	3.4	1.6
1991	37	62	4.8	3.0
1992	29	45	4.0	1.8

[a] Successful = at least one chick fledged.
[b] Includes some nests not in the core study area.

$t-1$, C_t = no. adults captured in year t, and A_t = no. adults available for capture in year t.

The following model was used to predict the size of the population in subsequent years beginning with the 1987 population (Brooks and Temple 1990):

$$N_t = N_{t-1}(S_a) + N_{t-1}(P/2)(S_j)$$

where N_t = size of breeding population in year t, N_{t-1} = size of breeding population in year $t-1$, S_a = survival rate of adults in year $t-1$ (from above), P = number of young fledged per breeding pair in year $t-1$, and S_j = survival rate of juveniles in year $t-1$. Because most surviving young left the study area to breed, it was not possible to estimate S_j in the same way that we could estimate S_a. Two values, 0.20 and 0.30, were therefore used in the modelling. We calculated the lower value from North American general banding returns of burrowing owls (Cave 1968). The higher value was used because this method tends to overestimate mortality (Newton 1979).

RESULTS

Over the seven-year study (Table 1), the proportion of owl pairs that produced at least one chick declined significantly ($r = -0.809$, $P < 0.05$). The number of chicks produced per successful pair, and per nesting attempt also declined, although not significantly ($r = -0.318$ and -0.584, respectively). Annual adult survival ranged between 37% and 51% (Fig. 1), and increased significantly over the period of study ($r = 0.857$, $P < 0.05$).

The population declined steadily from 76 pairs in 1987 to 29 pairs in 1992 (Fig. 2). The rate of decline was highly significant ($r = -0.976$, $P < 0.01$) and fairly constant. The equation of the regression line, $y = 82.8 - 9.5x$, predicts the extinction of the study population in about 1995, assuming that the decline remains linear. The simple population model (Brooks and Temple 1990) pre-

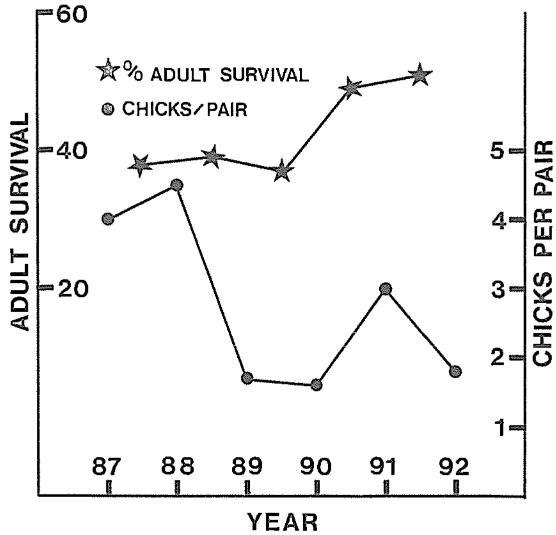

Figure 1. Annual adult survival of burrowing owls and chicks produced per nest attempt on the Regina Plain, Saskatchewan.

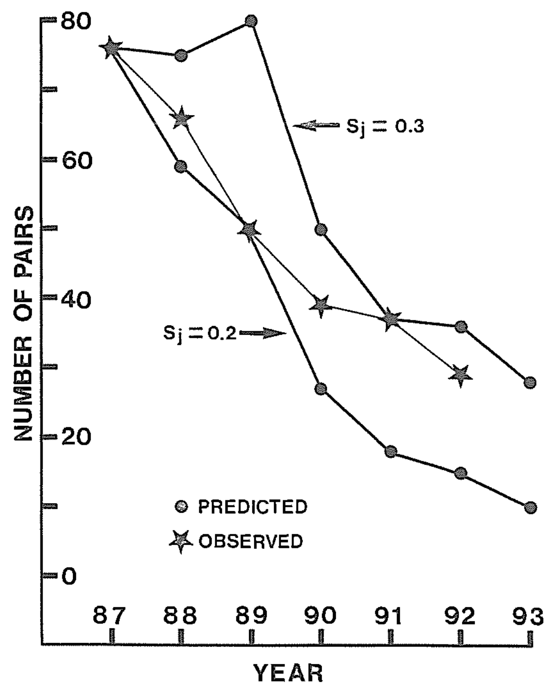

Figure 2. Observed and predicted decline of burrowing owls on the Regina Plain, Saskatchewan. Two predicted declines are shown.

dicted this decline quite well with juvenile survival somewhere between 0.20 and 0.30 (Fig. 2).

DISCUSSION

In no year were enough chicks produced to offset the measured adult mortality; hence, the predicted and observed population decline. Deciding the relative contribution of the three population parameters to this decline is somewhat difficult. Annual adult survival increased over the study period, but was it still too low in the absolute sense? The number of chicks produced per pair declined at the same time, and may have also been too low in an absolute sense. We believe that the adult survival was too low for two reasons. First, on a simple raptor body mass/adult mortality relationship (Newton 1979), our owls appeared to have a mortality rate greater than that expected from body mass alone. Second, our mortality estimates are similar to one calculated for another declining burrowing owl population (Johnson 1995), and much higher than those calculated for more stable populations (Thomsen 1971, Schmutz et al. 1988, Mealey 1997, Millsap and Bear 1995).

We also believe that in some years, the number of chicks produced per nest attempt was too low. Reviews of numerous other breeding productivity studies across North America have shown that the number of chicks produced per nest attempt has fallen below 2.0 only once (Zarn 1974, Haug and Didiuk 1991), yet this has occurred in three of seven years on our study area (Fig. 1).

Evaluating the relative role of juvenile survival is difficult because, unlike adult survival, we could not measure it on the study area owing to natal dispersal being much higher than breeding dispersal. However, if our adult survival and chick production estimates are reasonable, then juvenile survival of our population likely falls between 0.20 and 0.30 (Fig. 2). Based on other studies of more stable populations, this appears to be about right (Thomsen 1971, Millsap and Bear 1995). To investigate this further, we generated theoretical stable population lines by setting $N_t = N_{t-1}$ from the second equation above, and then solved for various values of S_j (Fig. 3). For our population to be stable with the observed adult survival and chick production, S_j would have to fall between 0.3 and 0.4, which is extremely unlikely to occur.

What then, is the cause for our low adult survival and poor chick production in some years? Canadian burrowing owls are migratory, but the location of their wintering grounds is still unknown (James 1992). Because juvenile survival appears normal (Fig. 2, and above discussion), the cause of the reduced adult survival and chick production is probably on the breeding grounds. Although some limiting factors have been evaluated (James 1993, James and Fox 1987, James et al. 1990, James et al. 1991), the role of predation has not. We believe that it could be important for the following reasons: (1) Complete brood failure levels are higher than other studies, and are increasing, while successful pairs have normal production (Table 1) consistent with a pattern produced by predation; (2) The habitat on the Regina Plain is now heavily fragmented, possibly making it easier for predators to find nests; research on nest predation has shown that it increases with increasing habitat fragmentation (Wilcove 1985, Terborgh 1989, Johnson and Temple 1990, Burger et al. 1994); (3) Several mammals that depredate nests of prairie birds, including burrowing owls, are very common in and around the study area (Sargeant et al. 1993).

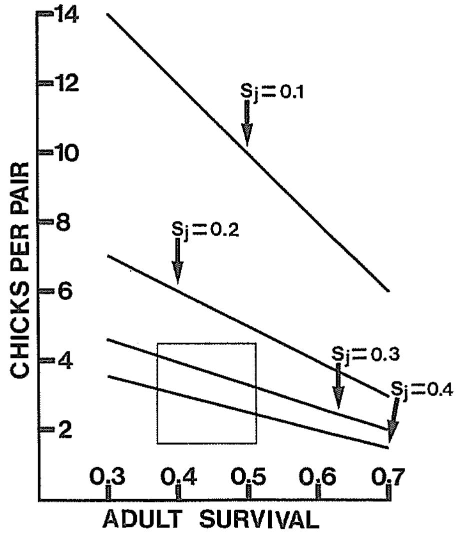

Figure 3. Theoretical stable population lines ($N_t = N_{t-1}$) for various values of S_j (juvenile survival). The window shows the observed values of adult survival and chicks produced per nest attempt on the Regina Plain, Saskatchewan.

We therefore hope, in the near future, to evaluate the role that predators may be playing in the decline of the burrowing owl in Saskatchewan.

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NOTE ADDED IN PROOF

The population continued its decline in 1993 as predicted in Fig. 2. In 1994, the Wildlife Branch of Saskatchewan Enviroment and Resource Management began a supplementary feeding program to boost the number of chicks produced. While still preliminary, the results indicate that the population has stabilized in 1995 and 1996.

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J. Raptor Res. Report 9:38–48

A CENSUS OF BURROWING OWLS IN CENTRAL CALIFORNIA IN 1991

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ABSTRACT.—The Institute for Bird Populations, with the help of 13 local Audubon Society chapters and ornithological organizations, conducted a census of burrowing owls (*Speotyto cunicularia*) in central California between 15 May and 15 July 1991. This 43 425-km^2 census area was divided into 1792 5-km by 5-km blocks oriented to the Universal Transverse Mercator system. Censuses were completed on a random stratified sample of 197 of these blocks and on 82 additional blocks that were not randomly chosen but were known to contain presumed breeding owls during the preceding decade. An analysis of these data suggests that: (1) the total breeding population of burrowing owls in the central California census area in 1991 may be estimated at about 873 pairs; (2) decreases of at least 23% of the breeding groups and 12% of the breeding pairs occurred during the five years 1986–91; (3) the rate of decline of breeding burrowing owls appeared to be greatest in the Outer Coast region, less in the Bay Area region, and least in the Central Valley region; (4) the number of pairs per breeding group also appeared to decrease, especially in the Bay Area region; and (5) the species was extirpated as a breeding bird from Sonoma, Marin, Napa, and Santa Cruz Counties during the decade 1981–91. We suggest that loss of breeding habitat may be a major cause for this population decline, but other factors may also have contributed to it. If the population trends indicated for the late 1980s continue, concerted efforts to reverse these trends will be necessary to prevent the species from becoming extirpated in central California.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *random stratified census; population estimate; population trends; California.*

Un censo del tecolotito enano en el centro de California en 1991

RESUMEN.—El Instituto de Poblaciones de Aves con la ayuda de 13 sociedades locales de Audubon y organizaciones ornitologicas condujo un censo del tecolotito enano, *Speotyto cunicularia* en el centro de California durante Mayo 15 a Julio 15 de 1991. El area censada que comprendia 43,425 km^2 se dividio en 1,792 cuadros de 5 km × 5 km orientados al sustema UTMS. Censos se completaron de manera estratificados al azar en 197 de los cuadros y 82 cuadros adicionales no seleccionados al azar sino en base al conocimiento de que estos contenian poblaciones reproductivas durante la decada anterior. El analisis de estos datos sugiere que: 1) La poblacion reproductiva total del tecolotito enano en el area censada en 1991 se estimo en aproximadamente 807 parejas; 2) Disminucion de cuando menos 23% de grupos reproductivos y 12% de parejas reproductivas occurio en los 5 años de 1986–1991; 3) La tasa de disminucion de tecolotes reproductores parece ser mayor en el area costera, menos en la region de la Bahia y menor en el area del Valle Central; 4) El numero de parejas reproductoras parece especialmente en el area de la Bahia; 5) La especie se ha extirpado como ave reproductora de los condados de Sonoma, Morin, Napa y Santa Cruz durante la decada de 1981–1991. Sugerimos que la principal causa de la disminucion de esta poblacion es la perdida de habitat reproductivo, pero otros factores pudieron haber contribuido. Si continua la tendencia indicada en los ultimos años de los 1980's esfuerzos concertados seran necesarios para prevenir que la especie sea extirpada del centro de California.
[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) is a characteristic species of flat, open grasslands at lower elevations nearly throughout California. The species has been undergoing a general population decline in California (and elsewhere in its range) for at least the past 60 years, generally as a result of "roadside shooting, anti-"vermin" campaigns, [and the] elimination of ground squirrels—hence of nesting places for these owls" (Grinnell and Miller 1944).

Within the past 20 years, however, the decline of burrowing owls in California appears to have accelerated, apparently as a result of habitat loss caused by the increased residential and commercial development of land that has paralleled the phenomenal growth of California's human population (McCaskie et al. 1979, Garrett and Dunn 1981). Indeed, it appears that certain characteristics of suitable burrowing owl nesting habitat (open, flat grassland at lower elevations) are very similar to the characteristics of land preferred for residential and commercial development. Because current indicators predict that California's extraordinary human population growth will continue during the 1990s and into the next century, the amount of burrowing owl habitat available and, thus, the size of burrowing owl populations in California can be expected to decline further.

The burrowing owl is currently classified by the California Department of Fish and Game as a "species of special concern," a classification that provides a stimulus for further study and a basis for limited habitat protection of the species. Although various individuals and organizations have suggested informally that a classification of "threatened" may be warranted, adequate data on which to base estimates of local, regional, and total population sizes as well as estimates of population trends are not available for burrowing owls in California. It is evident, therefore, that a census of California's burrowing owl populations, along with a follow-up program to monitor these populations, is justified.

A program of censusing and monitoring California's burrowing owls has a number of attractive components. Because burrowing owls are easily identified, relatively easily counted, and are favorite birds for many bird watchers, large locally-based volunteer efforts can provide accurate counts and exact locations for a substantial proportion of the local breeding populations, critical information on population changes, and useful data on habitat utilization for the species. Information on local and regional distributions and population changes of burrowing owls can be used to inspire local and regional planning processes that are crucial to the development of a sound conservation program for the species.

Detailed information on the exact numbers and locations of breeding burrowing owls over a substantial portion of their California breeding range during three consecutive years can be combined with detailed land-use information available from the California Department of Water Resources by means of Geographic Information Systems (GIS). These combined data can be used to define and evaluate the critical habitat requirements of the species, to estimate the total amount and distribution of potentially suitable habitat, and to estimate the total population size of the species. Such a technique has recently been used to estimate the total population size of the California gnatcatcher (*Polioptila californica*) (Atwood 1992).

In light of these considerations, we designed a three-year (1991–93) census and a follow-up, long-term monitoring program to determine population estimates and trends, to locate critical breeding areas, and to determine general habitat requirements for the burrowing owl in California. For practical and logistical considerations and in order to test the methods and refine the techniques, the first year of the census was limited to central California. The census was expanded in the second and third years to include all of the breeding range of the burrowing owl in California exclusive of the Great Basin and desert areas.

Here we report on the first year of the census, provide an estimate of the size of the 1991 breeding population in central California, and, based on previous anecdotal data on the numbers and locations of presumed breeding pairs, provide estimates of population trends for the species over the past half-decade (1986–91).

METHODS

Census Design and Sampling Considerations. The Institute for Bird Populations, in association with 13 local Audubon Society chapters and ornithological organizations in the San Francisco Bay area and the central part of the Central Valley of California, coordinated the establishment of a census of burrowing owls in central California. The focus of the 1991 census was an area of about 43 425 km^2 bounded by Sonoma, Napa, Yolo, Sacramento, and El Dorado Counties inclusive on the north; by Santa Cruz, Santa Clara, Merced, and Mariposa Counties inclusive on the south; by the 610-m contour line in the Sierra Nevada Mountains on the east; and by the Pacific Ocean on the west (Fig. 1). This area was apportioned among the 13 cooperating organizations according to their geographical areas of interest, which often were defined by county boundaries.

A local area coordinator was appointed by each cooperating organization. These area coordinators provided prior anecdotal information on breeding burrowing owls by plotting the exact locations and approximate numbers of all burrowing owls known or assumed to have bred in the area during the past five years (1986–90) on county

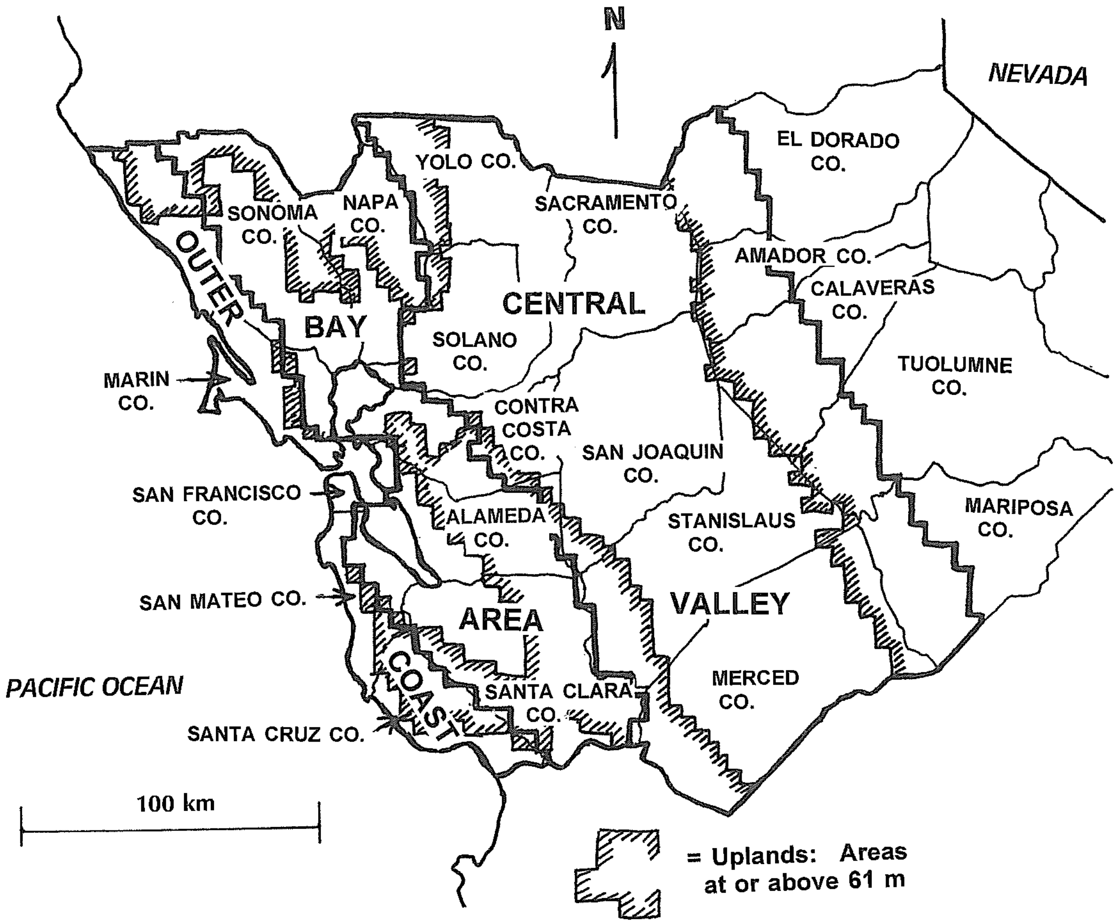

Figure 1. Map of the 1991 burrowing owl census area in central California showing the three geographic regions into which the census area was divided (Outer Coast, Bay Area, Central Valley) and the two elevation subregions into which each region was divided (lowland–below 61 m, upland–61 m and above).

(or other) maps. Locations of owls known or assumed to have bred in the area during the prior five years (1981–85), but that had disappeared by 1986, were also marked on the maps and indicated as such. Breeding at a given location was assumed if: (1) one or more adult owls were found during the breeding season (March–August); or (2) one or more owls were found during the non-breeding season (September–February), the nonbreeding-season location contained suitable breeding habitat, and historical information indicated that burrowing owls regularly bred in such habitats and at such locations in that general area of the county. Although the area coordinators used all available information to identify locations of presumed breeding (e.g., Suddjian and Rigney 1988), the compilations they supplied were understandably incomplete.

We divided the entire census area into three geographic regions (Fig. 1). The Outer Coast region extended west from the crest of the outermost coast range to the Pacific Ocean and also included most of Berkeley and northern Oakland. It thus coincided with those areas most heavily affected by extensive summer fogs. The Bay Area region extended east from the eastern edge of the Outer Coast region to the crest of the innermost coast range. This area encompassed most of the greater San Francisco Bay area and associated interior valleys, including the Petaluma, Sonoma, Napa, Walnut Creek, Livermore, and Santa Clara valleys. The Central Valley region extended east from the eastern edge of the Bay Area region to the 610-m contour line in the Sierra Nevada Mountains.

We divided each of these three geographic regions into two elevational sub-regions: that portion below 61 m and that portion 61 m and above (Fig. 1). In the central California census area under consideration, the 61-m elevation contour generally accurately discriminates between the relatively wide, flat lowlands and valley bottoms (where the vast majority of the agricultural and industrial

Table 1. Number of 5-km by 5-km census blocks (and % adequately completed) by geographic-elevation region and type for the 1991 census of burrowing owls in central California.

	RANDOM[a]			OWL[b]			TOTAL[c]		
	LOWLAND[d]	UPLAND[e]	TOTAL	LOWLAND	UPLAND	TOTAL	LOWLAND	UPLAND	TOTAL
Outer Coast	30 (86.7)	8 (87.5)	38 (86.8)	4 (75.0)	0 (—)	4 (75.0)	34 (85.3)	8 (87.5)	42 (85.7)
Bay Area	36 (80.6)	29 (62.1)	65 (72.3)	50 (72.0)	2 (50.0)	52 (71.2)	77 (74.0)	30 (63.3)	107 (71.0)
Central Valley	137 (65.7)	44 (61.4)	181 (64.6)	89 (79.8)	5 (80.0)	94 (80.0)	203 (69.0)	45 (60.0)	248 (67.3)
Total	203 (71.4)	81 (64.2)	284 (69.4)	143 (76.9)	7 (71.4)	150 (76.7)	314 (72.0)	83 (63.9)	397 (70.3)

[a] Blocks randomly selected (about 20% of lowland and 10% of upland blocks).
[b] Blocks that contained presumed breeding owls sometime during 1981–90.
[c] Because some random blocks previously contained breeding owls, the number of random blocks plus the number of owl blocks may be greater than the total number of blocks.
[d] Lowland blocks in which at least 5% of the area lay below 61 m elevation.
[e] Upland blocks lying above 61 m elevation.

development and a major portion of the residential development occurs) and the upland hills and mountains. The distribution of presumed breeding locations supplied by the area coordinators suggested that burrowing owl breeding habitat in central California may be essentially limited to the flat lowlands and valley bottoms of the area. The 61-m elevational division allowed us to test this hypothesis.

For sampling purposes, we divided the entire 43 425-km^2 census area into 1792 5-km by 5-km blocks oriented and referenced according to the Universal Transverse Mercator (UTM) system. We used a random number generator to chose 20% of the blocks in each geographic region (Outer Coast, Bay Area, Central Valley) that contained at least 125 ha (5% of its area) under 61 m elevation. A total of 203 of these "lowland blocks" was randomly chosen out of the 1012 total lowland blocks in the census area. We then randomly chose 10% of the blocks in each region that did not contain at least 125 ha under 61 m elevation, with the additional requirements that the chosen block contain at least 25 ha of open, nonscrub, nonforested area and that the block be accessible by automobile. A total of 81 of these "upland blocks" was randomly chosen out of the 780 total upland blocks in the census area. This gave us a total random stratified sample of 284 blocks termed "random blocks" (Table 1).

Next we plotted the locations where burrowing owls were presumed to have bred during the past ten years on five 1:250 000 scale U.S.G.S. maps that covered the census area and on which we had drawn the 1792 5-km by 5-km UTM blocks. These locations were found to occur in a total of 150 blocks which were termed "owl blocks" (Table 1). Thirty-seven of the 150 owl blocks (24.7%) had already been chosen as part of the sample of 284 random blocks; these were termed "random owl blocks." The remaining 113 owl blocks that were not chosen as part of the random sample, termed "non-random owl blocks," were then added to the random sample of 284 blocks and produced a total sample of 397 census blocks. The remaining 247 random blocks in which owls were not presumed to have bred during the past ten years were termed "random non-owl blocks."

We marked and physically cut the 397 5-km by 5-km UTM census blocks out of 1:24 000 scale U.S.G.S. topographic maps (7.5-min series). These cut-out census blocks were each placed in packets that also included a "locator map" (a portion of a 1:250 000 scale U.S.G.S. map), a specially-prepared 12-page instruction and information booklet on censusing burrowing owls, and appropriate data sheets. We apportioned the 397 census blocks among the 13 cooperating organizations and distributed the completed packets to the area coordinators who, in turn, distributed them to volunteer censusers that they recruited. To provide in-the-field instruction and training for both the area coordinators and the volunteer censusers, four half-day training sessions were held prior to the census in late April.

Field Work. The volunteer censusers were asked to cover all of the area in their blocks at least once during early-morning (dawn to 1000 H) or late-afternoon (1600 H to dusk) hours during the 2-mo period between 15 May and 15 July, when breeding burrowing owls were likely to be feeding nestlings or recently-fledged young. During these times, one or both parents are usually readily observable at or near the mouth of the nest burrow. Censusers were asked to search their blocks as thoroughly as possible for burrowing owls, and to operate under the assumption that burrowing owls are, or should be, present, and that the censuser's job is to find them or to prove that they are not there.

Censusers were asked to classify the various areas contained in their block into one of three categories depending on the extent of their coverage of them: inadequate, adequate, or thorough. Areas were considered adequately covered if a reasonable effort was made to search all locations where burrowing owls were likely to be breeding. Areas were considered thoroughly covered if the censuser felt confident that her/his estimate of the number of breeding pairs of owls was correct and that all breeding owls were located. Censusers were also asked to provide a narrative and standardized information on the amount and timing of effort they expended on their block.

Censusers were asked to provide: (1) a count of all owls seen in their block, identified, if possible, to age and sex; (2) an estimate of the number of nesting pairs; (3) the exact locations of all owls seen plotted directly on the U.S.G.S. topographic map of their block; and (4) standardized habitat information at all locations where they found owls.

Data Analysis. We transcribed the exact locations of all burrowing owls presumed to have bred in the census area during the previous ten years (1981–90) directly onto the completed U.S.G.S. 7.5-min topographic maps of each of the owl blocks. Because we wanted to obtain an unbiased population estimate from the random sample of blocks and did not want to bias the coverage of owl blocks, particularly the coverage of random owl blocks, we did not transcribe prior owl locations onto maps before sending them out for censusing.

We used data from the 1991 census to obtain estimates for the total number of breeding pairs of burrowing owls in 1991 in each geographic-elevation region and then summed these estimates to obtain an estimate for 1991 for the entire census area. We used two methods to obtain these regional estimates. In the first method, we used data from all random blocks but did not use data from nonrandom owl blocks. We estimated $N1_i$, the total number of pairs of owls in the ith (geographic-elevation) region from Method I as $N1_i = nr_i * (1/pr_i)$ where nr_i is the total number of pairs counted in 1991 in all of the random blocks that were adequately or thoroughly censused in the ith region and pr_i is the proportion of the total area of the ith region that was contained within all of the random blocks in the ith region and that was adequately or thoroughly censused.

In the second method, we used data from only the random non-owl blocks (rather than from all the random blocks) and then added data from the owl blocks. In this case we estimated $N2_i$, the total number of pairs of owls in the ith region from Method II as $N2_i = N2n_i + N2o_i$ where $N2n_i$, the total number of pairs in all the non-owl blocks in the region, is calculated as $N2n_i = nrn_i * (1/prn_i)$ where nrn_i is the total number of pairs counted in 1991 in all of the random non-owl blocks that were adequately or thoroughly censused in the ith region and prn_i is the proportion of the total area of all the non-owl blocks in the ith region that was adequately or thoroughly censused, and where $N2o_i$, the total number of pairs in all owl blocks in the region, is calculated as $N2o_i = no_i * (1/po_i)$ where no_i is the total number of pairs counted in 1991 in all of the owl blocks that were adequately or thoroughly censused in the ith region and po_i is the proportion of the total area of all the owl blocks in the ith region that was adequately or thoroughly censused. Those portions of the blocks that fell in the Pacific Ocean or San Francisco Bay were not included in calculating any of the areas used in these estimations.

Estimates of the total number of breeding pairs of owls obtained from these two methods in any region will differ somewhat depending on the distribution of owls in the region and the proportion of owls whose locations were actually known prior to the 1991 census. If owls tended to be underdispersed (clumped) in any region and the locations of a large proportion of the owls in the region were known prior to the 1991 census, estimates from Method II will generally be larger and probably more accurate. This was likely the situation in the Bay Area and Outer Coast regions. In contrast, in areas where the owls tended to be overdispersed (more uniformly distributed) and a relatively small proportion were known prior to 1991 (as was probably the case in the Central Valley region), Method I will generally produce larger and probably more accurate estimates. We estimated the total population size of breeding owls in the entire census area by summing the larger of the two estimates for each region over all six geographic-elevation regions.

Finally, we used data provided by the area coordinators on the presumed breeding locations of burrowing owls in the census area in the 5-yr period 1986–90, coupled with the results of the 1991 census, to estimate changes in the numbers of breeding pairs of owls between these two time periods in each of the three geographic regions and for the census area as a whole. Because burrowing owls appear to move their breeding sites over short (2–3 km) distances from year to year as conditions change, but do not appear to move over larger distances (A. Huffman and D. DeSante unpubl. data), we apportioned all of the known and presumed breeding locations of burrowing owls into "breeding groups." Any location found within 3.0 km of any other location in continuous breeding habitat, or within 2.0 km of any other location from which it was separated by non-breeding habitat, was considered to be part of the same breeding group. This procedure effectively apportioned breeding locations into breeding groups; in fact, most owl locations were found to lie either well within 2 km or well over 3 km of each other.

We then used these breeding groups as the appropriate units to determine population changes from the 1986–90 period to 1991. We calculated the number and proportion of groups that disappeared by 1991, that remained in 1991, and that were newly found in 1991. Then, for each region and for the entire census area, we calculated changes in the numbers of groups and in the numbers of pairs in each of these groups. Because the data for the 1986–90 period were not derived from a systematic census but rather from anecdotal information, many of the new groups and pairs within those new groups that were found in 1991 were likely present during 1986–90 but were unknown at that time. Thus, we calculated changes between 1986–90 and 1991 in the numbers of groups and pairs by two methods: (1) including and (2) excluding data from newly-found groups.

RESULTS

Effort Expended. A total of 279 blocks (70.3% of the 397 blocks sent out) was adequately or thoroughly censused during the summer of 1991 (Table 1). In addition, 9 blocks (2.3%) were censused and returned but the effort over the entire block was considered inadequate. An additional 85 blocks (21.4%) were returned but not censused, and 24 blocks (6.0%) were never returned. It is likely that most of these 24 outstanding blocks were not censused. A total of 2111 person-hours was spent surveying the 279 adequately-censused blocks for an average effort of 7.57 hr per block. In all, a total area of 6195 km^2 was adequately

Table 2. Estimates of the numbers of breeding pairs of burrowing owls in the central California census area in 1991.

	OUTER COAST		BAY AREA		CENTRAL VALLEY		
	LOWLAND[a]	UPLAND[b]	LOWLAND	UPLAND	LOWLAND	UPLAND	TOTAL
I. Method I (using all random blocks)							
nr (pairs in random blocks)	0	0	9	0	86	1	96
pr (proportion of area censused)	0.170	0.080	0.143	0.062	0.123	0.052	
N1 (estimate of total population)	0.0	0.0	62.8	0.0	698.0	19.1	
II. Method II (using random non-owl blocks and all owl blocks)							
A. Estimate in non-owl blocks							
nrn (pairs in random non-owl blocks)	0	0	0	0	27	1	28
prn (proportion of area censused)	0.185	0.080	0.131	0.062	0.109	0.047	
N2n (estimate in non-owl blocks)	0.0	0.0	0.0	0.0	247.9	21.5	
B. Estimate in owl blocks							
no (pairs in all owl blocks)	0	0	98	5	205	0	308
po (proportion of area censused)	0.817	—	0.687	0.500	0.753	0.520	
N2o (estimate in owl blocks)	0.0	0.0	142.7	10.0	272.3	0.0	
C. Estimate in total census area (A + B)							
N2 (estimate of total population)	0.0	0.0	142.7	10.0	520.2	21.5	
III. Final estimate (using larger estimate for each region)							
N (estimate of total population)	0.0	0.0	142.7	10.0	632.2	21.5	806.4
n (total pairs found in 1991)	0	0	98	5	232	1	336
% pairs known in 1991	—	—	68.7	50.0	36.7	4.7	41.7

[a] Lowland blocks in which at least 5% of the area lay below 61 m elevation.
[b] Upland blocks lying above 61 m elevation.

searched for burrowing owls during the 1991 census. Table 1 shows that overall the Outer Coast received somewhat better coverage (85.7% of blocks adequately censused) than the Bay Area (71.0%) and Central Valley (67.3%), lowland blocks received slightly better coverage (72.0%) than upland blocks (63.9%), and owl blocks received slightly better coverage (76.7%) than random blocks (69.4%).

Number of Owls Found and an Estimate of the Total Breeding Population. No breeding burrowing owls were found in 1991 in the Outer Coast region, 103 pairs were found in the Bay Area region, and 233 pairs were found in the Central Valley region, resulting in a total of 336 pairs in the total census area (Table 2). Fully 330 of these 336 pairs were found in lowland blocks.

Estimates derived from two methods (see Methods section) for the number of breeding pairs of burrowing owls in 1991 in each of the six geographic-elevation regions and in the total central California census area are presented in Table 2. As perhaps expected, Method II (using random non-owl blocks and owl blocks separately) gave higher estimates for all regions except the Central Valley lowlands where many owls still exist but relatively few of them were previously known. Indeed, Method I actually underestimated the known numbers in regions where most of the owls were already known, as was the case in both Bay Area subregions.

Using the larger of the estimates from the two methods for each region, Table 2 estimates that, as of 1991, no breeding pairs of burrowing owls existed in the Outer Coast region, only about 153 breeding pairs existed in the Bay Area region, and only about 720 breeding pairs existed in the Central Valley region, resulting in a total of only about 873 breeding pairs in the entire central California census area. Moreover, as of 1991, the locations of 67.5% of the pairs estimated to be present in the Bay Area region, 32.4% of those estimated to be present in the Central Valley region, and 38.5% of those estimated to be present in the entire census area were known.

Apparent Population Decline of Breeding Burrowing Owls in the Census Area. The 1991 census failed to find burrowing owls in 59 (51.3%) of the 115 owl blocks that were adequately censused and returned, suggesting that, in the 10 years 1981–90, the proportion of the census area occupied by breeding burrowing owls decreased by about 50%. Indeed, our data indicate that, as of 1991, burrowing owls had been extirpated as breeding birds from Sonoma, Marin, Napa, and Santa Cruz Counties.

These results, however, do not necessarily imply that a 50% decline has occurred in the total population of breeding burrowing owls in central California. Rather, it is possible that owls are now occupying blocks in which they were formerly absent and that the 50% decline in occupied owl blocks represents a shifting of the population rather than a population decline. Such a scenario, however, seems unlikely to account for the number of blocks from which owls disappeared, because previously unknown owls were found in 1991 in only 15 (9.1%) of the 164 random non-owl blocks adequately censused. Moreover, all 15 of these "new owl blocks" were located in the Central Valley region where the distribution of owls was relatively poorly known prior to the 1991 census. In contrast, three of the 59 blocks from which all owls disappeared were located in the Outer Coast region and 21 were located in the Bay Area region. Furthermore, owls were not found in 1991 in any of the 33 random non-owl blocks adequately censused in the Outer Coast region nor in any of 39 similar blocks in the Bay Area region.

It is also possible that the blocks from which burrowing owls disappeared were areas of somewhat marginal habitat that previously supported only a few breeding pairs and that the total number of breeding pairs in central California has not declined precipitously. We can test this hypothesis by analyzing changes between the 1986–90 period and 1991 in the actual numbers of breeding groups (as defined in the Methods section) and pairs of owls. As discussed in the Methods section, this analysis was accomplished in two ways, first by excluding and then by including blocks in which owls were not known prior to 1991 but were found in 1991.

The results of these analyses indicate that, when new owl blocks were excluded, the changes in the number of breeding groups of owls (Fig. 2A) were −100.0% for the Outer Coast region, −54.5% for the Bay Area region, −48.3% for the Central Valley region, and −51.8% for the entire census area. When new owl blocks were included in the analysis, the changes in the number of breeding groups of owls were −100.0% for the Outer Coast region, −50.0% for the Bay Area region, −8.6% for the

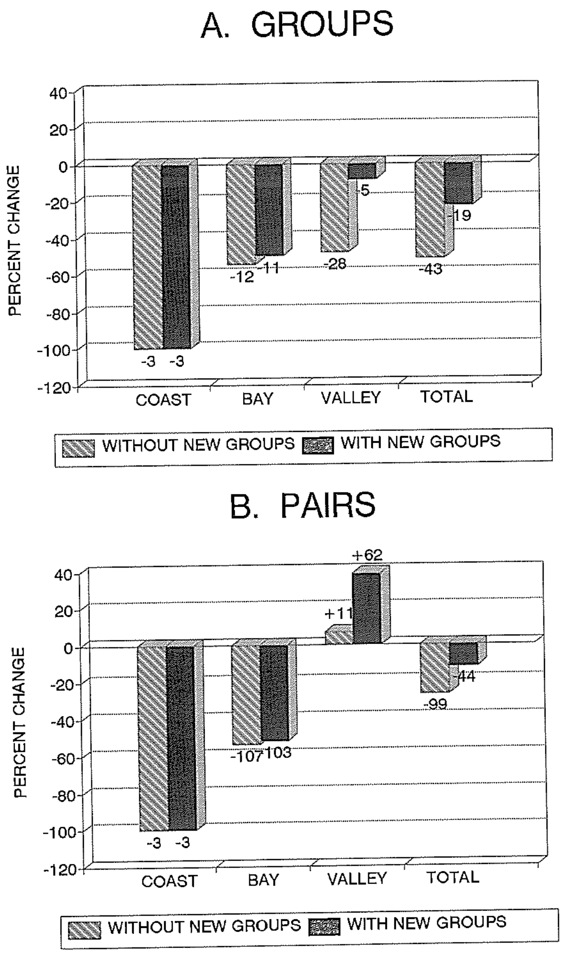

Figure 2. Percent changes in the numbers of (A) groups and (B) pairs of burrowing owls from the 1986–90 time period to 1991 for each geographic region (Outer Coast, Bay Area, Central Valley) and for the entire central California census area (Total). Changes were calculated by two methods: excluding and including newly-found groups of owls (see text). Numbers below (or above) each bar are the actual changes in numbers of groups or pairs.

Table 3. Estimates of the number of pairs of burrowing owls per breeding group obtained from the 1991 census and anecdotal information during the prior five years (1986–90).

	OUTER COAST		BAY AREA		CENTRAL VALLEY		TOTAL	
	1986–90	1991	1986–90	1991	1986–90	1991	1986–90	1991
For groups that disappeared	1.00	—	2.67	—	1.36[a]	—	1.70[b]	—
For groups that remained	—	—	16.60	9.10	4.10[a]	5.73	7.22[b]	6.58
For newly-found groups	—	—	—	4.00	—	2.22	—	2.39
For all groups combined	1.00	—	9.00	8.64	2.78[a]	4.21	4.36[b]	4.97

[a] Probably biased low because of very incomplete information on the numbers of pairs breeding previously.
[b] Probably biased low because of low-biased estimates from the Central Valley region.

Central Valley region, and −22.9% for the entire census area. The smaller decreases found when new owl blocks were included, especially in the Central Valley region, reflects the fact that not all breeding groups of owls were known prior to the 1991 census. The actual rates of change probably lie somewhere between the extremes produced by the two methods. Anecdotal information supplied by area coordinators further describes the disappearance of 14 presumed breeding owl groups in the Bay Area region and 11 in the Central Valley region between the 1981–85 and 1986–90 time periods. This indicates that the apparent decline of owls was already underway during the first half of the past decade.

Changes in the number of breeding pairs of owls (Fig. 2B), when new owl blocks were excluded, were −100.0% for the Outer Coast region, −54.0% for the Bay Area region, +6.8% for the Central Valley region, and −27.3% for the entire census area. When new owl blocks were included in the analysis, the changes in the number of breeding pairs of owls were −100.0% for the Outer Coast region, −52.0% for the Bay Area region, +38.5% for the Central Valley region, and −12.2% for the entire census area. Again, the smaller decreases (or larger increases in the Central Valley region) found when new owl blocks were included reflects the fact that the actual numbers of breeding pairs of owls were very poorly known prior to the 1991 census, especially in the Central Valley region. The actual rates of change again probably lie somewhere between the extremes produced by the two methods. And again, anecdotal information supplied by area coordinators describes the disappearance of 22 presumed breeding pairs of owls in the Bay Area region and 11 in the Central Valley region between 1981–85 and 1986–90.

Estimates of the number of pairs of burrowing owls per breeding group (group size) were obtained from the 1991 census and from anecdotal information during the prior five years, 1986–90 (Table 3). In each geographic region, group size was smallest for groups that disappeared, intermediate for newly-discovered groups, and largest for groups that remained. This suggests that groups that disappeared were smaller than average, probably were previously reduced in size, and possibly tended to be located in marginal habitats or near the edges of the species range in central California. Group size for groups that remained decreased markedly between 1986–90 and 1991 in the Bay Area region and over the entire census area but appeared to increase in the Central Valley region. This latter apparent increase was probably caused by the fact that group size was very poorly known in the Central Valley prior to the 1991 census and likely was seriously underestimated. For example, in the Central Valley, the number of pairs at many of the presumed breeding locations that were mapped by the area coordinators were not known; in these cases, we assumed that only one pair of owls was present at a breeding location. The overall reduction in group size between 1986–90 and 1991 for groups that remained suggests that population decreases also occurred in optimal habitats and in the heart of the species' range in central California as well as in marginal habitats and on the periphery of the range.

DISCUSSION

Estimate of the Total Breeding Population. Results of the 1991 census indicate that the total 1991 population size of burrowing owls in the central California census area was small, perhaps only about 873 pairs, and that the locations of a substantial proportion of these (a total of 336 pairs, 38.5%) were known in 1991. Information on these known pairs will be very important in efforts to protect the owls, and every effort should be expended to locate as many as possible of the remaining pairs of owls in central California.

In addition, only three groups comprising six total pairs of owls were found in only two blocks that lay entirely above 61 m in elevation; two of these groups and five of these pairs were located in a single block in the Livermore area. This block was, in fact, the only block in the entire Bay Area region where breeding owls were found substantially removed from the immediate vicinity of San Francisco Bay. These results confirm that very few burrowing owls breed in central California at elevations above 61 m, and that the species seems to be virtually confined to the flat, lowland portion of the Bay Area and Central Valley regions. Such areas, moreover, are the areas that are being increasingly used for new residential and commercial development.

It is also of considerable interest that burrowing owls were apparently extirpated as breeding birds during the past decade from Sonoma, Marin, Santa Cruz, and Napa Counties, and only one breeding pair apparently still existed in San Mateo County in 1991. The population around the north end of San Francisco, San Pablo, and Suisun Bays was also reduced to a very small remnant, if indeed it still existed at all. It appears, therefore, that breeding burrowing owls in central California have been, or very soon will be, reduced to only three isolated populations: a moderate but declining population of about 720 pairs in the Central Valley, a small and rapidly declining population of about 143 pairs in the lowlands around the southern arm of San Francisco Bay between Alameda and Redwood City, and a very small, isolated population of about 10 pairs in the Livermore area. Such population fragmentation will very likely further increase the species' risk of extirpation.

Estimates of Recent Population Change. The results of the 1991 census, coupled with anecdotal information from 1986–90, suggest that the net population change between these two time periods was a decrease of about 23–52% in the number of breeding groups and about 12–27% in the number of breeding pairs of owls. A more exact estimate of population change cannot be obtained because of the incomplete and anecdotal nature of the information on breeding burrowing owls prior to the 1991 census. The overall decreases of both breeding groups and breeding pairs, however, appeared to be greatest in the Outer Coast region (100% for both groups and pairs), less in the Bay Area region (about 53% for both groups and pairs), and least in the Central Valley region (perhaps about 28% for groups and an increase of about 23% for pairs). It seems likely that the loss of most of these breeding groups and many of these breeding pairs was caused primarily by the loss of breeding habitat.

Data from the 1991 census and prior anecdotal information during the period 1986–90 suggest that the number of pairs per breeding group (group size) also decreased in at least the Bay Area region (and probably also in the Central Valley region). This suggests that some other factors in addition to habitat loss may be contributing to the decrease in burrowing owls in central California. Although we have no direct data to support the hypothesis, we suspect that various agricultural practices, including removal of ground squirrels, use of chemical herbicides on levees along irrigation canals, and the more general use of chemical insecticides and rodenticides may also be contributing to the observed declines of burrowing owls in central California.

Such agricultural practices could adversely affect the productivity and survivorship of burrowing owls. In this regard, it may be worth noting that the number of young fledged from burrowing owl nests in central California in recent years seemed to vary between three and six, with most nests fledging only four or five young (pers. obs.). Anecdotal accounts of nesting burrowing owls in California during the first half of this century suggest that six to eight young were usually fledged (Dawson 1923). Indeed, other avian predators in central California, including loggerhead shrike (*Lanius ludovicianus*), American kestrel (*Falco sparverius*), and Swainson's hawk (*Buteo swainsoni*), also appear to be declining as breeding birds in recent years in central California (R. Stallcup pers. comm.). The first two species, like burrowing owls, rely heavily on large insects in their diet during the breeding season and forage in similar grassland habitats.

Sources of Error in Estimates of Population Size and Change. A number of factors could have contributed to errors in this census: (1) limitations of the pre-1991 data that were supplied to us by the area coordinators; (2) inaccuracies in the 1991 census itself; and (3) misinterpretation of the data from the 1991 census. It must be stressed that 1991 was the first year of an organized, comprehensive census of burrowing owls in central California and any comparison of the 1991 data with the qualitatively different data from the previous years involves uncertainty. Nevertheless, the pre-1991 data can be viewed as a sample of known breeding locations from which qualified estimates of population change can be derived.

The limitations of the pre-1991 data can lead to three types of errors. First, some of the pre-1991 presumed breeding locations may not have been actual breeding locations but may have represented only wintering or transient birds. Second, because the pre-1991 data spanned five years, owls present at some of the locations in a given year may have been the same individuals recorded at different locations less than 2–3 km away in other years. Both of these errors will bias the pre-1991 number of breeding pairs toward the high side. On the other hand, the actual number of breeding pairs was not known for many of the pre-1991 breeding locations, especially in the Central Valley. This undoubtedly biased the pre-1991 number of breeding pairs toward the low side. The effects of these three biases may have tended to cancel each other.

The most likely error in the 1991 census data was that some owls were missed by the volunteer censusers. Although burrowing owls are generally quite easy to locate, they are cryptically colored and can be very difficult to see, especially if the grass around their nesting burrows is dense and tall. It is likely, therefore, that the actual number of breeding owls in the census area in 1991 could have been somewhat higher than the calculated estimate of 873 pairs. Similarly, the actual rate of decline in the number of pairs of burrowing owls between 1986–90 and 1991 could have been somewhat lower than the calculated estimate of 12–27%.

A final source of error could arise from misinterpretation of the 1991 census data, particularly if burrowing owls move their breeding locations from year to year by more than 2–3 km, such that some of the 55 new pairs of owls in some of the 24 new owl groups were actually previously-known owls that had disappeared from locations more than 2–3 km away. It is worth stressing, however, that only 64 groups totaling 318 pairs of breeding owls were found in 1991 in the adequately-censused portion of the entire census area, despite the fact that 2111 person-hours were spent searching 6195 km^2 for owls. Considering that as many as 83 groups totaling 362 pairs of breeding owls were previously known from this portion of the census area, the 1991 census data provides evidence for a decrease of at least 22.9% of the groups and 12.2% of the pairs of breeding owls during the 5-yr period 1986–91. This translates to a rate of decline for groups of about 4.6% per year and for pairs of about 2.4% per year.

Thus, despite the limitations of using pre-census owl data to estimate the decrease in the numbers of breeding owls in the census area and the uncertainties as to the exact accuracy of the 1991 census, it is obvious that burrowing owls have suffered substantial decreases in the numbers of both breeding groups and breeding pairs in central California in the past decade. This, coupled with estimates of a small total population size, portends a bleak future for the species in central California. Furthermore, anecdotal information on the status of burrowing owls elsewhere in California suggests that similar declines may be occurring in other regions as well. Clearly, a concerted attempt to identify the locations of most of the remaining breeding pairs of burrowing owls in California, along with a comprehensive monitoring program for the owls, is required to provide the detailed information necessary to design an effective recovery plan for the species in California.

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ADDENDA

In order to provide additional estimates of population size and more rigorous estimates of population change, we duplicated the 1991 census of central California in both 1992 and 1993. Preliminary analyses of these data suggest that the number of breeding groups in the entire census area decreased by 16.7% from 1991–92 and remained constant from 1992–93, while the number of breeding pairs increased by 3.1% from 1991–92 and decreased by 5.2% from 1992–93. These data suggest that the number of breeding groups continued to decline substantially during the early 1990s while the number of breeding pairs declined only slightly during that time period, presumably because of excellent breeding success in 1991. In addition, the census area was expanded in 1992 and 1993 to include all of the remainder of the Sacramento and San Joaquin Valleys, the Coachella and Imperial Valleys, and the entire coastal slope of southern California from Monterey County to the Mexico border. Preliminary analyses of data from this expanded census area further confirmed the small and declining nature of burrowing owl populations throughout the remainder of the breeding range of the species in California.

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SEASONAL RECORDS OF THE BURROWING OWL IN MEXICO

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ABSTRACT.—I compiled data on 279 burrowing owls (*Speotyto cunicularia*) from 27 museums. The earliest burrowing owl specimens from Mexico are from 1840. Most individuals were collected from 1900–10. Sixty-three percent of specimens were from the non-breeding (wintering) season. The burrowing owl has a wide distribution in Mexico; it is located in 28 of 32 Mexican states. *S. cunicularia* has been the third most common owl collected in the country. Baja Peninsula has provided the most specimens; specimens are lacking for the southeastern region. The high number of individuals collected during the winter season suggests that Mexico is an important wintering area for burrowing owl populations.

KEY WORDS: *burrowing owl*; Speotyto cunicularia; *Mexico*; *distribution*; *breeding*; *museum specimens*.

Registros estacionales del Tecolote Zancón en México.

RESUMEN.—Se compiló un total de 279 datos del tecolote zancón (*Speotyto cunicularia*), provenientes de 27 museos. Las primeras colectas se registraron en 1840. La mayoría de los individuos se colectaron en la década de 1900–1910. El 63% de los especímenes se registraron en la temporada no reproductiva. El tecolote zancón presenta una amplia distribución en México, se localizó en 28 estados de la República Mexicana. *S. cunicularia* ha sido la tercer especie de búho más colectada en el país. La Península de Baja California contuvo el mayor número de especímenes y la región del sureste sohresalió por la falta de ellos. El elevado número de individuos presentes en la temporada no reproductiva, sugiere un incremento de las poblaciones del tecolote zancón en México, pudiendo ser este país una importante área de invernación.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) has a wide distribution in the western hemisphere, from southern Canada through South America, to Tierra del Fuego (A.O.U. 1983). Burrowing owls inhabit open lands and grasslands (Johnsgard 1988), nest in abandoned burrows, and exhibit both diurnal and nocturnal habits. In recent decades, the Canadian and U.S. burrowing owl populations have been decreasing because of several factors (James and Fox 1987, Weseman and Rowe 1987). This owl species has been listed in the Blue List since 1972 in the U.S.A. and classified as threatened in Canada (James and Ethier 1986). Principal reasons for the decline are loss of grassland habitats, use of insecticides, rodent poisoning programs, limited nest burrows, and shooting (Schmutz 1991).

Populations that breed in northern portions of the range winter south of the U.S.-Mexico border (James 1992). Although some banded northern burrowing owls have been recovered in Mexico and Central America, little is known about breeding and nonbreeding distributions in Mexico. In this paper, I discuss both historical and seasonal records and distribution of Mexican burrowing owls.

STUDY AREA AND METHODS

I obtained burrowing owl data from six national (Colección Ornitológica del Instituto de Biología, Colección Ornitológica de San Nicolás de Hidalgo-Univ. Michoacán, Escuela Nacional de Ciencias Biológicas, Instituto de Historia Natural de Chiapas, Instituto Nacional de Investigaciones sobre Recursos Bióticos, and Salón de las Aves de Saltillo Coahuila) and 21 foreign museums (British Museum, Bell Museum of Natural History, Carnegie Museum of Natural History, Cornell University Collection, Delaware Museum of Natural History, Museum of Natural History-Chicago, Forschungsinstitut und Naturmuseum Senckenberg, Harvard Museum of Comparative Zoology, Illinois State Museum Collection, Kansas University Collection, Los Angeles, California Museum of Natural History, Louisiana State University Museum of Zoology, Moore Laboratory of Zoology-Occidental College, Museum of Vertebrate Zoology-University of California Berkeley, National Museum Smithsonian Institute, Provincial Museum of Alberta, Rijksmuseum Van Natuvrlijke Historie-Leiden, Royal Ontario Museum, San Diego Museum of Natural History, Western Foundation

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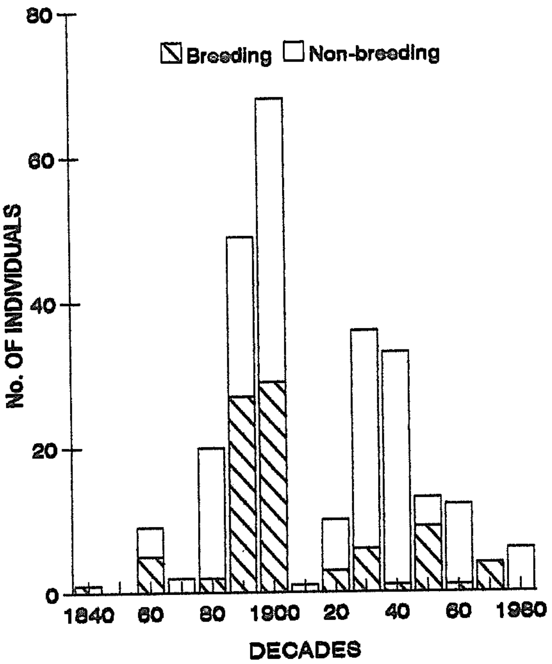

Figure 1. The number of burrowing owl specimens collected in México from 1840s through 1980s.

Vertebrate Zoology Collection, and Zoological Institute of the Academy of Sciences-Moscu).

Data were divided into two seasons: breeding (16 April–15 October) and nonbreeding (16 October–15 April) and analyzed by decades. Based on these data, I prepared a distribution map with breeding and nonbreeding ranges.

RESULTS

I compiled data on 279 burrowing owls. The earliest burrowing owl record found was collected in the 1840s. Most individuals were collected between 1900 and 1910 (Fig. 1), followed by 1890s (n = 49), 1930s (n = 36) and 1940s (n = 33). Sixty-three percent of the individuals were collected in the nonbreeding (wintering) season, and 37% were from the breeding season (Fig. 1). More than 80% collected since 1930 were from the nonbreeding (wintering) season, but recent decades (1960s, 70s and 80s) have produced only 8% of the total specimens.

Specimens were collected from 26 states (Fig. 2). Burrowing owls also have been recorded in Nuevo Leon (Friedman et al. 1950) and Durango (Rodríguez-Estrella pers. comm.), so I included these states in the distribution map. The Mexican state of Durango was included in the breeding range due to reports on nest-site selection by burrowing owls in that state (Rodríguez-Estrella and Ortega-Rubio 1992).

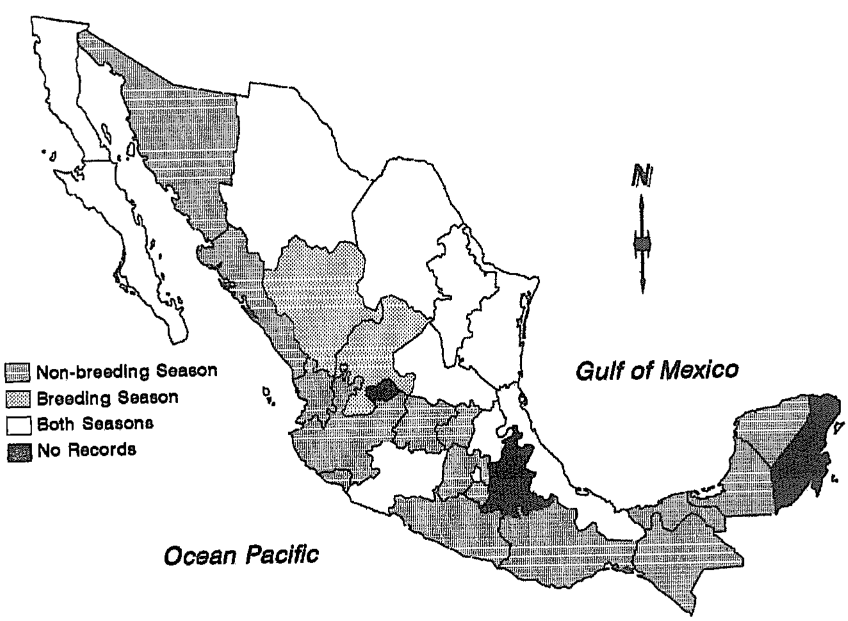

Figure 2. Burrowing owl distribution map showing breeding and nonbreeding areas in México.

Baja California has provided the most specimens (n = 61), followed by Colima (n = 36), Guerrero (n = 18), Sinaloa (n = 13) and Tamaulipas (n = 13). The other states provided from 1–11 specimens. The southeastern region stands out for a lack of information (Oaxaca [n = 5], Chiapas [n = 3], Tabasco [n = 11], Campeche [n = 1], Yucatán [n = 1], and no records for Quintana Roo). Although the state of Colima had 36 specimens, most of them were from Clarion Island (n = 27), in the Pacific Ocean. This land contains the subspecies *Speotyto cunicularia rostrata*, whereas the subspecies found on the mainland is *S. cunicularia hypugaea* (Ridgway 1914).

DISCUSSION

In Mexico the burrowing owl has a wide distribution, being recorded in 28 of the 32 states. It is the third most common owl species in the country, based on museum specimens (Enríquez 1990). The high number of specimens from the nonbreeding season suggests an increase of burrowing owl numbers during winter, probably due to the arrival of North American migrants. The increase in owl specimens from the winter season could also be accounted for by the arrival of ornithologists who migrate with the neotropical migrant birds. Nonetheless, existing records of the museum owl specimens may also depend on variables such as habitat, area, and time of day of capturing, as well as method and effort of capture by each collector.

The burrowing owl has been recorded in most Mexican states, but there are no records for the states of Aguascalientes, Puebla, Tlaxcala or Quintana Roo. Reasons for lack of specimens in these states are unknown, especially because there is no evidence of lack of suitable habitat.

Only breeding records were found in Durango and Zacatecas (Fig. 2). Excluding Michoacán and Baja California, only nonbreeding (wintering) data were located in the Pacific region, as well as in some central states and in the southeastern Gulf of Mexico (including the Yucatan Peninsula). Both breeding and nonbreeding records were found in northern Mexico, Baja California, and some states from the Gulf of Mexico.

In Mexico, breeding and wintering areas have not been well described. Also, the status of Mexican owl populations, as well as migration routes of northern populations, and the relative importance of factors affecting populations, continue to be unknown. I propose to begin an intensive program to record reports of burrowing owls. This program should establish a computer base center, and also facilitate plotting maps to determine the best conditions for burrowing owls. Both reports and maps will help identify preferred and/or priority use areas. In parallel with these efforts, a network should be established which involves researchers who are banding on both breeding and nonbreeding grounds, defining migration routes, determining resident populations and, perhaps, achieving other goals. Additionally, studies should be started on the ecology of owls at wintering areas establishing the effects of human activities and determining if this impact is contributing to the species' decline.

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I am greatful to all museum managers who kindly provided me with Mexican owl specimen data and my enthusiastic husband, J. Luis, who helped with the writing and English translation. Thanks to J. Espinoza, J. Lincer, R. Clark, R. Rodríguez-Estrella, and K. Steenhof for their comments on the manuscript.

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ECOLOGY OF THE BURROWING OWL IN AGROSYSTEMS OF CENTRAL ARGENTINA

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ABSTRACT.—Studies on the ecology of the burrowing owl (*Speotyto cunicularia*) in agrosystems of central Argentina were conducted: (1) to record basic information on habitat use, food habits, differential predation on rodents, feeding strategy, and breeding biology; (2) to examine reproductive success and conservation needs; and (3) to examine the owl's regulatory effects on rodent populations. The burrowing owl is a generalist predator, and its diet strongly depends on the availability of alternative prey. It showed differential predation by species and size of rodents and a functional response to changes in the abundance of rodent populations. Nests are built in areas with relatively low disturbance. Reproductive success was as low as 0.3 fledged per brood. Brood size negatively affected the growth of chicks. Main mortality factors for eggs were agricultural practices and predation, and for chicks were illness and hunting. The low reproductive success of the burrowing owl suggests a declining population. Strategies for conservation should be initiated as soon as possible.

KEY WORDS: *burrowing owl; ecology;* Speotyto cunicularia; *Argentina; management; prey; agriculture; breeding biology; growth.*

Ecologia del tecolotito enano en agrosistemas de Argentina Central

RESUMEN.—Se realizaron estudios de la ecología de la lechucita vizcachera (*Speotyto cunicularia*) en agrosistemas de Argentina central con los objetivos de: (1) recopilar información básica acerca del uso del habitat, predación diferencial sobre roedores, estrategia alimentaria y biología reproductiva; (2) examinar el éxito reproductivo y las necesidades de conservación; y (3) examinar los efectos regulatorios de la predación sobre las poblaciones de roedores. La lechucita vizcacahera es un predador generalista cuya dieta depende de la disponibilidad de presas alternativas. Mostró una predación diferencial por especie y tamaño de roedores y una respuesta funcional a los cambios en la abundancia de roedores. Los nidos son contruidos en áreas con perturbaciones relativamente bajas. El éxito reproductivo fue muy bajo, 0.3 juveniles por puesta. El tamaño de la puesta afectó negativamente el crecimiento de los pichones. Las principales causas de mortalidad de huevos fueron las labores agrícolas y la predación, y de la mortalidad de pichones fueron las enfermedades y la caza. El bajo éxito reproductivo sugiere que esta población de lechucitas está declinando y que estrategias de conservación deberían iniciarse lo antes posible.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) may be found in almost all grassy plains of Argentina (Olrog 1978) and is common in agrosystems. Studies on the ecology of the burrowing owl in agrosystems of central Argentina started in the early 1980s. Initially, studies focused on burrowing owl predation on rodents because some rodent species were involved in human diseases and crop damage. The first step was to develop an accurate method to identify species, age, and sex of rodents found in pellets. After having this tool, studies dealt with diet and its seasonal changes, differential predation on rodent populations, and functional response. Later, evidence suggested a declining population of the burrowing owl, and subsequent studies focused on breeding biology and management. Here, I provide a review of the studies conducted by me on the ecology of the burrowing owl in agrosystems of central Argentina, setting priorities for future research.

STUDY AREA

Studies were conducted approximately 100 km northwest of Buenos Aires city, province of Buenos Aires, Ar-

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gentina (34°18'S, 59°14'W) during 1982–88. The study area was located in the Pampa region in the east central part of the country. The region shows moderate weather conditions, with a mean daily temperature of 9.8°C in winter and 22.5°C in summer, and an annual mean precipitation of 946 mm varying from 130 mm in winter to 306 mm in summer (INTA 1972). The area was originally a natural prairie. Having highly productive soils, it was subsequently and completely used for agrarian activities since the beginning of the nineteenth century. Today, the northern portion of the region, where these studies were conducted, is devoted mostly to farming (especially cereal crops) with a few areas used for ranching. Three main kinds of habitat may be distinguished: (1) cultivated fields that experience strong perturbations due to farming; (2) fields with natural grass used for grazing cattle; and (3) margins of cultivated fields, extremely narrow corridors that show relatively low disturbance.

Food Habits. The diet of the burrowing owl and its seasonal changes were studied in detail for one year (Bellocq 1988a). A total of 1176 pellets collected during 1982–85 were qualitatively analyzed to identify prey items to the level of Order. Rodent species were quantified in the content of 609 pellets (140 pellets collected in spring, 83 in summer, 231 in fall, and 150 in winter) following Bellocq and Kravetz (1983). A detailed quantification of the diet was conducted for a subsample of 128 pellets (26 collected in spring, 26 in summer, 44 in fall, and 32 in winter). Data on the number and biomass of prey consumed were analyzed by season.

Differential Predation on Rodents. The consumption and abundance of rodent species, size, and sex were compared to determine whether the burrowing owl preyed differentially on rodent populations (Bellocq 1987, Bellocq and Kravetz in press). Relative abundance of rodent species, size, and sex was estimated by livetrapping. Eighteen Sherman trap lines were set in fields and margins (total effort-1400 trap nights). Traps operated from 1–7 June 1984, when rodents were most abundant in the field (for details on field methods see Bellocq 1987). Captured rodents were identified and classified into three groups (juveniles, sub-adults and adults) according to their mass (Bellocq and Kravetz 1994). Consumption of rodents by the burrowing owl was estimated by pellet analysis (113 and 164 pellets to study predation by rodent species and by size-sex, respectively). Species, size categories, and sex were identified from pellets using molars and pelvis (Bellocq and Kravetz 1983). Identifications, especially sex, were not possible in some cases because the molars were absent or the pelvis broken. Regressions between body mass and tooth wear allowed prediction of rodents mass found in pellets (Bellocq 1988b). Manly's alpha (Chesson 1978) was used to obtain food preference indices.

Functional Response. Abundance of rodents was estimated monthly by livetrapping in approximately 100 ha during 1984. Consumption of rodents by burrowing owls was also estimated monthly by analyzing pellets collected in the same area as the trapping was conducted (see Bellocq 1988b for details on field methods). Regression analysis was performed between the number of rodents per pellet and the abundance of rodents in the field.

Effects of Agricultural Practices on Rodent Predation by Burrowing Owls. The effects of harvest and plowing

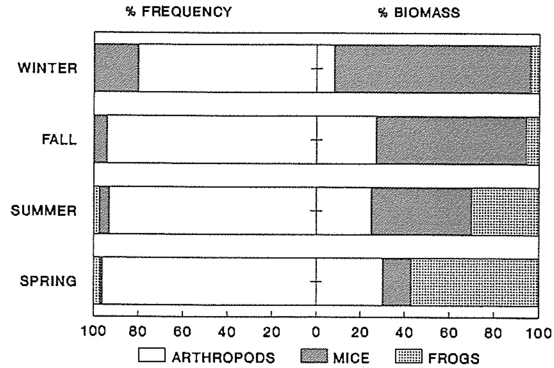

Figure 1. Percentage frequency of the number of prey items (N = 791) and percent biomass of arthropods, mice, and frogs found in pellets of burrowing owls, and their seasonal changes in agrosystems of central Argentina.

on rodent predation by the burrowing owl were examined as part of a project to assess the effects of agricultural practices on rodent populations (de Villafañe et al. 1988). Abundance of rodents was estimated using a grid of Sherman traps in a cornfield during four periods, pre- and post-harvest and pre- and post-plowing. Consumption of rodents was estimated by analyzing pellets of burrowing owls whose burrows were closer than 500 m from the experimental cornfield during the same periods as the trapping was conducted.

Breeding Biology. Some aspects of the breeding biology of the burrowing owl were observed during 1983–87 and recorded in 1988 (Bellocq 1993). Seven nests with eggs were followed during the breeding season, and the brood size, reproductive success, and mortality factors were recorded for each nest. Chicks were weighed every 2–5 days and growing curves were constructed. Seven artificial nest burrows (Collins and Landry 1977) were set in margins of fields grazed by cattle and checked weekly for one year.

RESULTS

Diet. The burrowing owl was a generalist predator in agrosystems of central Argentina (Bellocq 1988a). Its diet contained a large number of different prey including arthropods (beetles, grasshoppers, spiders, etc.), small mammals (mice, bats, etc.), and frogs, snails, snakes, birds, etc. Most of these prey, however, occurred only occasionally in the diet. The main food consisted of arthropods, mice, and frogs. In terms of the number of prey items consumed year round (total number of prey 791 in 128 pellets), arthropods represented 91% of the diet, rodents 8%, and frogs 1% (Fig. 1). In terms of biomass, however, rodents and frogs were more important than arthropods. Based on a total

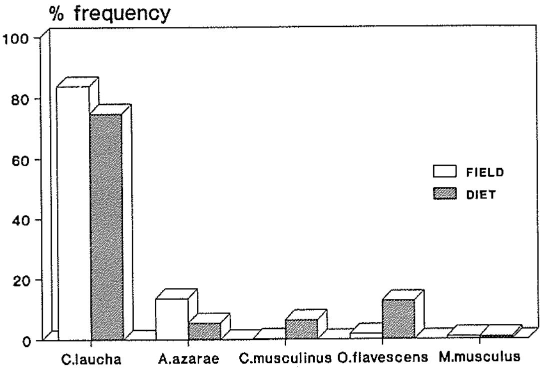

Figure 2. Percentage frequency of the number of rodents (N = 111) by species in the field and in the diet of the burrowing owl in agrosystems of central Argentina.

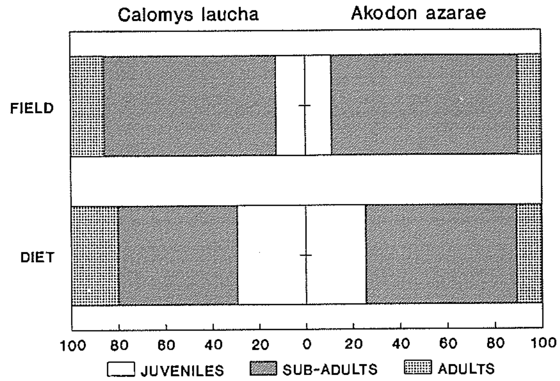

Figure 3. Percentage frequency of the number of *Calomys laucha* (N = 116) and *Akodon azarae* (N = 47) by size categories in the field and in the diet of the burrowing owl in agrosystems of central Argentina.

of 343 rodents identified in 609 pellets, *Calomys laucha* was the most common species (67%) followed by *Akodon azarae* (12%), *Calomys musculinus* (10%), *Oligoryzomys flavescens* (10%), and *Mus musculus* (1%).

The proportion of food types in the diet showed seasonal changes. The number of rodents per pellet, e.g., increased from 0.1 in the spring to 1.1 in the winter while the number of frogs per pellet dropped from 0.2 in the spring to 0.02 in the winter. This showed a shift in the diet typical of generalist predators.

Differential Predation on Rodents. Burrowing owls preyed preferentially on rodent species (Bellocq 1987). The number of individuals of different rodent species found in pellets (total number of identified individuals was 111 in 113 pellets) was independent of their abundance in the field (X^2 = 244.8, $P < 0.001$). *Oligoryzomys flavescens* and *C. musculinus* were the preferred species; whereas *A. azarae* was eaten in a lower proportion than expected based on trap captures (Fig. 2). *Calomys laucha* was taken in a similar proportion to what was available in the field.

The burrowing owl showed differential predation on rodents by size categories (Bellocq and Kravetz 1994). The observed frequencies of size categories of rodents in the diet (total 116 *C. laucha* and 47 *A. azarae* found in 164 pellets) were different from the expected based on trap captures (X^2 = 36.9, $P < 0.001$ and X^2 = 9.2, $P < 0.02$, for *C. laucha* and *A. azarae,* respectively). Food preference indices showed that burrowing owls preyed on medium-sized rodents in a lower proportion than expected according to their relative abundance. Juvenile rodents were eaten more than expected while large-sized adults were taken as expected (Fig. 3). The analysis of predation by sex (based on 27 *C. laucha* identified in 164 pellets) showed burrowing owls took females and males *C. laucha* according to the estimated sex ratio (X^2 = 0.6, $P > 0.1$) (Bellocq and Kravetz in press).

Functional Response. Analysis of the availability and consumption of rodents during one year showed that burrowing owls responded functionally to the abundance of rodents in agrosystems of central Argentina (Fig. 4) (Bellocq 1988b). The mean number of rodents per pellet depends on the abundance of rodents (R^2 = 0.747, F = 20.53, $P < 0.005$).

Effects of Agricultural Practices. Results showed that harvest and plowing increased the impact of owl predation on rodents (de Villafañe et al. 1988). After harvest, the mean number of rodents per pellet increased 10 times while the abundance of rodents was similar in the pre- and post-harvest periods (Table 1). The number of rodents per pellet was similar during the pre- and post-plowing periods whereas the abundance of rodents in the field decreased after plowing.

Breeding Biology. Nests were found in areas with relatively low disturbance. The agricultural systems on this land include rotations in seeding which result in some fields laying fallow from several months to a few years. Most nests of burrowing owls were found in these kinds of fields, in small areas with short grass around farms, and in mar-

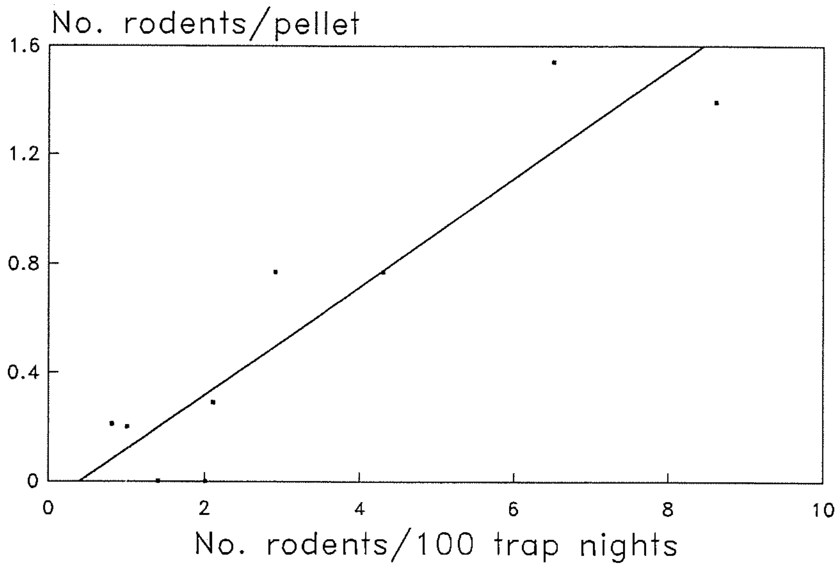

Figure 4. Functional response of the burrowing owl to changes in the abundance of rodents in agrosystems of central Argentina.

gins. In general, burrows were located close to fence posts. Nests were placed at the terminal portion of the burrows and their floors were covered with dry cattle dung. Artificial nest burrows were not colonized by burrowing owls.

Eggs were laid in mid-spring (October–November), followed by hatching in mid-November to early December (Bellocq 1993). The average clutch size was 4.8 ± 1.2 eggs (mean ± 1 SD), and the mean number of hatchlings per nest was 3.5 ± 2.4. Reproductive success was as low as 0.3 fledged per brood. Of the total number of eggs ($N = 32$), 66% of them hatched and only 10% of the total number of hatchlings ($N = 21$) survived to fledge.

Table 1. Abundance of rodents and number of rodents per pellet during the pre- and post-harvest and pre- and post-plowing periods in a cornfield.

	No. rodents/ 100 Trapnights	No. rodents/ Pellet
Harvest		
pre-treatment	14	0.04
post-treatment	12	0.41
Plowing		
pre-treatment	8	0.80
post-treatment	1	0.81

Main mortality factors of eggs were agricultural practices and predation (presumably by marsupials), and main causes of chick mortality were illness and hunting.

Brood size negatively affected the growth of chicks (Bellocq 1993). Although hatching was generally synchronized, older chicks grew faster than younger chicks in the same clutch (Fig. 5). Similarly, chicks belonging to smaller broods grew faster than chicks belonging to larger clutch sizes ($F = 4.74$; $P < 0.05$ for broods of 2, 3, 4, and 5 chicks 8-d-old, and $t = 4.18$, $P < 0.01$ for broods of 2 and

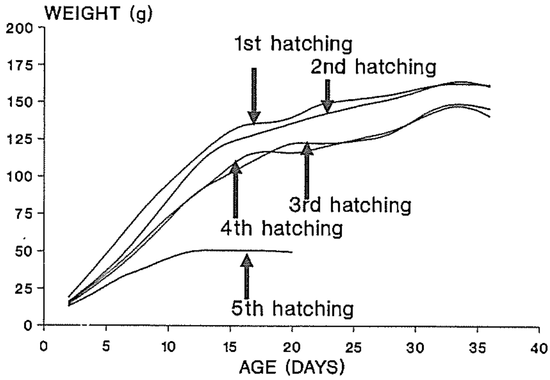

Figure 5. Growth curves of five burrowing owl chicks belonging to the same brood.

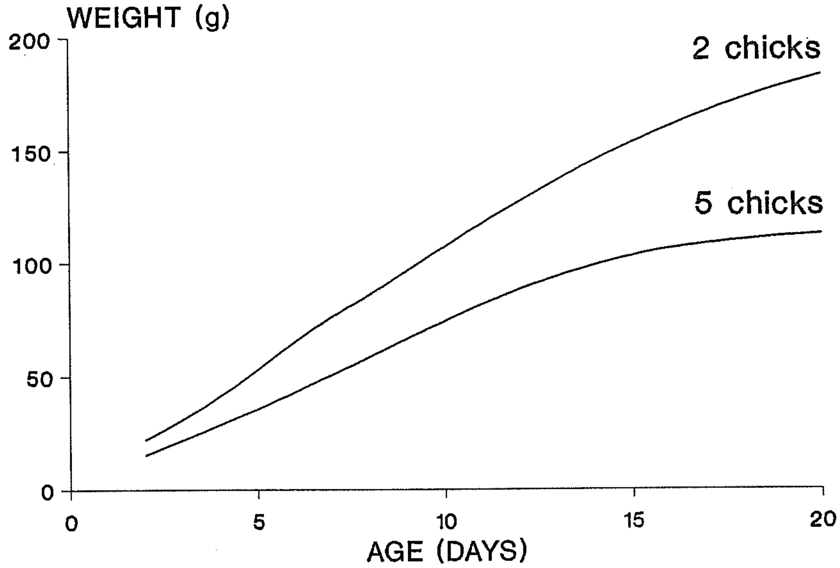

Figure 6. Mean growth curves of chicks belonging to broods of two and five chicks.

5 chicks 20-d-old, respectively) (Fig. 6). Chicks weighed 9.5 g at 1 day and reached 170 g in 20 days. They fed mainly on insects and frogs, and started to fly at approximately 40–50 days of age.

DISCUSSION

The biomass provided by different types of food varied seasonally. Rodents were the main source of food responsible for the winter survival of burrowing owls. Although most of the small mammals found in pellets were mice, the burrowing owl is able to prey on larger mammals in this area, like *Ctenomys talarum* and *Cavia pamparum* (Pearson et al. 1968, de Villafañe et al. 1988). During the breeding season, frogs were the primary food. Because brood size had a negative influence on the growing of chicks, food supplement might help to improve body condition and increase survival of chicks.

The burrowing owl showed an opportunistic feeding behavior. Consumption of rodents increased, whereas consumption of frogs decreased from spring to winter, following changes in the abundance of both kinds of prey in the fields. The burrowing owl's choice of juvenile rodents may be explained by the high vulnerability of juveniles, supporting the argument of an opportunistic feeding behavior. Selection of rodents by size categories may be linked with differences in rodent vulnerability by age or social hierarchy. Generally, adult rodents (socially dominant) display territorial behavior that decreases predation risk through increasing knowledge of the habitat and the ability to escape from predators (Metzgar 1967). Thus, juvenile rodents would be more vulnerable to predation than adults.

Burrowing owl predation on rodents increased as the abundance of rodents increased. This suggests that the burrowing owl might contribute to the regulation of rodent populations. It is a generalist predator and presumably resident all year round. Moreover, the environment provides a good supply of alternative prey. Although studies on dispersal and migration were not conducted in this area, observations showed that the burrowing owls may be seen all year round in agrosystems of central Argentina. However, numerical response to the abundance of rodents may occur when rodents increase some years. Increasing the numbers of burrowing owls may result in increased predation on rodents and contribute to the biological control of rodents involved in human diseases and crop damage.

Artificial nest burrows were not colonized showing that the availability of nesting sites is unlikely a limiting factor of burrowing owl population growth in agrosystems of central Argentina. However, availability of suitable nesting habitat and quality of nesting sites may be negatively affecting reproductive success. Burrowing owl nests are mainly found in fields with natural grasses that are uncommon in the northern part of the Pampa region. Leaving small patches of natural grass surrounding croplands would provide additional nesting habitat. When plowing, a small area surrounding the existing nests could be left untouched. Burrows used for nesting are frequently short (the shortest found was about 30 cm long) which may increase vulnerability to predation and hunting. Likely because of this, and in contrast with most North American observations, burrowing owls in the study area leave their nests when humans or animals approach the nest (they only remain in the nest when eggs are close to hatching or chicks are younger than approximately 10-d-old). Alternatives to improve quality of nest sites should be analyzed and implemented. For instance, nest quality was the primary cause of mortality of barn owl (*Tyto alba*) chicks in the study area (chicks fell down from human constructions). Productivity of the barn owl, however, was improved 50% by setting artificial nest boxes (Bellocq and Kravetz 1993).

In agrosystems of Argentina, future research should be oriented toward long-term studies (population dynamics, reproductive success, key mortality factors) and development of management strategies. The low reproductive success documented here suggests that this population may be declining drastically, and that strategies for conservation should be put in place as soon as possible. Some suggestions on habitat management were provided above, but regulations should be developed together with educational programs.

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GENETICS AND BREEDING BIOLOGY

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CHARACTERIZATION OF POPULATION AND FAMILY GENETICS OF THE BURROWING OWL BY DNA FINGERPRINTING WITH pV47-2

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ABSTRACT.—Genetic attributes of the burrowing owl (*Speotyto cunicularia*) were revealed by DNA fingerprinting with the minisatellite probe pV47-2. I report here on DNA fingerprint variability, fingerprint inheritance and rate of mutation, and population substructuring. Each genetic profile comprised an average of 28.9 highly variable, somatically stable Mendelian markers, and contained single-locus, as well as multilocus, banding patterns, depending on hybridization stringency. Individual fingerprint specificity was minimally 8.4×10^{-17}, with an estimated mutation rate of 0.005. Allelic and genotypic frequencies at the pV47-2 locus indicated genetic substructuring within a pool of several geographically separated burrowing owl populations from western North America, and within a pool of populations from California, as well as inbreeding in an intensively-studied California burrowing owl population. These results suggest that nonrandom breeding and population subdivision in this species may be occurring at very fine spatial scales, levels of inbreeding may be elevated, and burrowing owl genetic effective population size may be small. If local populations are genetically and demographically isolated from one another, local extinctions may be exacerbated, and recolonization from extant burrowing owl populations will be less likely.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *DNA fingerprinting, avian genetics.*

Caracterizacion genetica de poblacion y familiar del tecolotito enanon usando huellas de ADN con pV47-2

RESUMEN.—Atributos geneticos del tecolotito enano (*Speotyto cunicularia*) se evaluaron con huellas de ADN con el minisatelite pV47-2. Aqui reporto la varibilidad de huellas de ADN en la herencia de huellas y el grado de mutacion y en la subsestructura de la poblacion. Cada perfil genetico comprendio un promedio de 28.9 marcadores Mendelianos somatico estables con alta variabilidad y contenian patrones de bandas con sitios unicos y sitios multiples, dependiendo en el grado de hibridacion. Especificidad de huellas individuales fue minima 8.4×10^{-17}, con una taza de mutacion de 0.005. Frequencias alelicas y genotipicas en el sitio pV47-2 indico subestructura genetica dentro del caudal de varias poblaciones de tecolotito enano separadas geograficamente del resto de Norte America y dentro de un caudal de California asi como intracruzamiento en una poblacion intensamente estudiada en California. Estos resultados sugieren que la repoduccion no al azar y subdivision de la poblacion esta ocurriendo a escala espacial muy fina, que los niveles de intracruzamiento pueden ser elevados y que la poblacion geneticamente efectiva del tecolotito enano puede ser chica. Si poblaciones locales estan geneticamente y demograficamente aisladas de las demas, extinciones locales se pueden exagerar y recolonizacion de poblaciones existentes es poco probable.

[Traducción de Filepe Chavez-Ramirez]

A major goal of my research (Johnson 1996a,b) is to characterize genetic and demographic parameters in order to examine the basis of population dynamics, population structure, and breeding systems in the social fossorial burrowing owl (*Speotyto cunicularia*). Because burrowing owls conduct a substantial portion of critical behaviors underground or at night, comprehensive direct observations are often not feasible. Consequently, the

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first step in these studies was to develop genetic techniques that would reveal in detail the mating systems, genealogies, and patterns of reproductive success in wild burrowing owl populations.

Because the interpretation and utility of hypervariable genetic markers depends on assumptions of Mendelian inheritance, somatic stability, linkage equilibrium, and a high degree of polymorphism, and because these assumptions may not always hold (Burke and Bruford 1987, Jeffreys and Morton 1987, Jeffreys et al. 1987), empirical tests need to be made, where possible, of markers that result from various combinations of species, DNA probe, and analytical conditions (see Epplen 1991). I report here on pV47-2 fingerprint variability in burrowing owls, and on fingerprint inheritance, rate of mutation, and population substructuring.

METHODS

I analyzed DNA from three subgroups of North American burrowing owls. I collected the largest number of blood samples (from 18 adults and 49 young) from a wild population of burrowing owls in Davis, California, in 1987–88, during the fieldwork described by Johnson (1996a,b). In 1987 I obtained another California sample from a group of wild owls (10 individuals, including two putative sibships) being held by the Santa Clara Humane Society prior to local translocation in Santa Clara County, California. Two other burrowing owl families (five individuals in each) from a Canadian captive-breeding project (Owl Rehabilitation Research Foundation, Vineland, Ontario) composed the third sample, collected in 1990. This was the only group available to me in which each adult pair had been reproductively isolated from others, ensuring exclusive parentage. The captive adults used in these controlled matings came originally from Manitoba, Idaho, and Wyoming, locations too disparate to be combined for a thorough analysis of population genetic structure. However, the samples were useful for the study of the inheritance of DNA fingerprint patterns, unconfounded by unknown matings.

Nuclear DNA was isolated by standard protocols (Maniatis et al. 1982, Ausubel et al. 1987) from blood collected from each burrowing owl by brachial venipuncture. The DNA was cleaved with HinfI and size-fractionated in 0.6% agarose gels run at 30 V for 44 hrs in recirculating TBE. Hybridization with minisatellite probe pV47-2 (provided by J. Longmire, Los Alamos National Laboratory; Longmire et al. 1990) was generally performed as described by Westneat et al. (1988) for M13 bacteriophage probes. All blots were washed at low stringency in 2 × SSC/0.1% SDS, once for 15 min at room temperature and once for 15 min at 60°C. After exposure to Kodak X-Omat AR film for 1–3 d, the blots were subsequently washed at high stringency with 0.5 × SSC/0.1% SDS at 60°C.

DNA fingerprint analysis was automated by high-resolution transmissive camera scanning using a Bio Image digitizing system consisting of a Sun/Sparc2 Workstation, Visage software, and a Megaplus VME-interfaced camera capable of converting an autoradiograph into a 1024 × 1024 pixel image. In the images used for this analysis, resolution was ultimately limited by the fact that one camera pixel unit corresponded to about 100 bp at high molecular weights (e.g., 20 kb) and to about 5 bp at 2.3 kb.

To estimate the frequency of DNA fragments and "alleles," I collapsed the distribution of band sizes into larger size categories, or bins (see Budowle et al. 1991 for the general procedure). I used three different binning strategies (see Table 1), based on (1) variation among replicates on different gels, (2) differences in the sizes of homologous bands across one gel (calculated from the known pedigrees), and (3) resolution of the digitized images.

Table 1. Binning strategies for determination of fragment and allele frequencies.

	BIN SIZES (BP) BASED ON		
MW RANGE (BP)	VARIATION AMONG GELS	VARIATION WITHIN GELS	IMAGE RESOLUTION (PIXELS)
15 870–23 130	400	230	100
9416–15 870	285	140	60
6682–9416	169	70	40
4361–6682	120	45	15
2322–4361	76	28	15

RESULTS

Inheritance. DNA fingerprints were inherited as somatically stable Mendelian markers. Ninety-one clearly resolved unique parental bands were scored in the two captive-bred owl families. Those fragments known to be inherited by only some progeny were transmitted on average to about half of the offspring of each parent ($\bar{x}$ = 53.7% ± 2.83% SE), generally in agreement with a 1:1 segregation ratio. I compared the number of offspring that received each unique parental fragment to the expected binomial distribution, assuming 50% transmission. The data for all adults combined were consistent with binomial expectations (*G*-test with Williams' correction, $P < 0.006$).

Mutation. The mutation rate per locus per generation was estimated to be 0.005. In DNA fingerprints from the two captive burrowing owl families with known pedigrees, only one of 212 offspring bands was novel, in that it did not correspond to fragments detected in either of its parents.

Multilocus Fingerprints. Multilocus DNA fingerprints were highly polymorphic. Hybridization of burrowing owl DNA with pV47-2 revealed a diverse array of fragments in the molecular weight range of 1.5–25.0 kb in all samples. At low stringency an average of 28.9 fingerprint bands (±5.30 SD) could be resolved per individual (N = 87). In the captive burrowing owl families, an average of 62% of parental bands were transmitted to some offspring. There was no single fingerprint band size, among the 462 resolved by the smallest binning scheme (absolute image resolution), that appeared in all individuals sampled. Even when I grouped bands in a manner which accommodated maximum among-gel error, the frequency of a few size categories (each of which might actually have represented one fragment size) approached , but did not exceed, 76%.

Locus-Specific Bands. When the blots were washed at high stringency, only one or two bands (in the homozygous or heterozygous case, respectively) remained in each lane at positions between 16 and 23 kb. This pattern can be most parsimoniously interpreted as being due to a single locus possessing a large number of alleles. Based on bin (allele) sizes that were derived from variation among sample replicates on different gels, at least 15 alleles exist at this locus and the mean frequency of an allele is 0.1138 (±0.0856 SD). Alternatively, using bin sizes based on absolute image resolution suggests up to 50 alleles at this locus, with a mean allele frequency of 0.0392 (±0.0321 SD).

Fingerprint Individuality. Individual specificity of DNA fingerprints is based on the premise that fragments having the same mobility (hence the same size) in different individuals represent the same allele (Geursen 1990). Under this simplifying assumption, the frequencies of fragment occurrence in hypervariable multilocus fingerprints are analogous to multilocus allele frequencies. I calculated the estimated average probability p, that an allele present in one burrowing owl is also present in another, from the proportion of individuals possessing a fragment in a particular bin size category (Jeffreys et al. 1985b, Geursen 1990, Kirby 1990). Using the two most extreme binning criteria, I was able to derive a range of values for p from the DNA fingerprints of 27 presumably unrelated burrowing owls (adults, all populations). Binning based on variation among gels resulted in a minimum of 102 bins (alleles), with a mean frequency of 0.2778 (±0.1930 SD) per allele in the population, whereas binning based on image resolution suggests at least 531 bins, with frequency averaging 0.0625 (±0.0510 SD). I calculated a range for the probability p^n, that two random burrowing owls could share a DNA fingerprint, where n is 28.9, the average number of bands per individual. The chance of two unrelated burrowing owls having the same pV47-2-detected multilocus fingerprint therefore appears to lie between 8.4×10^{-17} and 1.6×10^{-35}.

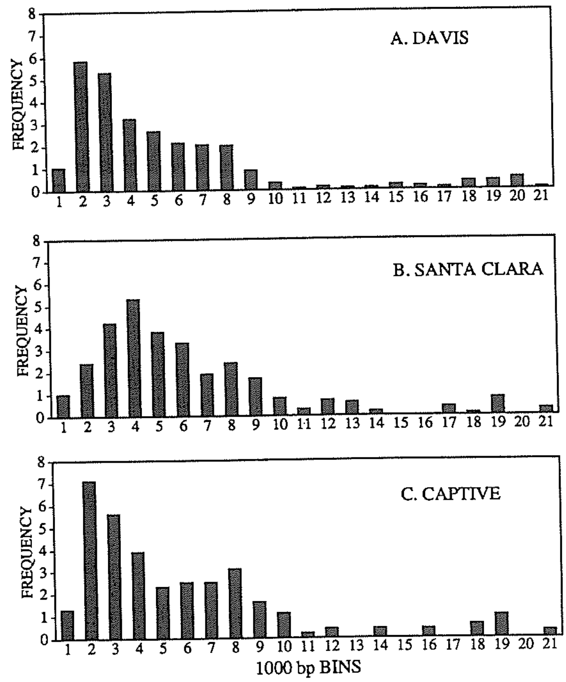

Figure 1. Frequency distributions of multilocus DNA fragments from individuals sampled from three geographically separated burrowing owl populations (A. Davis, CA: n = 67; B. Santa Clara, CA: n = 10; C. Captive: n = 10). Bands (putative alleles) were combined in 1000 bp bins. Most bins were represented in all samples; bins 15 and 20 were unique to the Davis population.

Population Comparisons. Coarse size distributions of multilocus fragments in the Davis, Santa Clara, and Canadian captive-breeding ("Captive") populations are shown in Fig. 1, where bands have been combined in 1000 bp bins. All three distributions are bimodal. Binned fragments in the Santa Clara and Captive samples (Fig. 1B,C) fall within the size range of alleles detected in the Davis sample (Fig. 1A). Most bins are represented in all groups, and the only bins unique to a sample were bins 15 and 20, which are only represented in the Davis sample.

At the single locus I analyzed sample substructuring by the method of Chakraborty et al. (1991),

Table 2. Test for Hardy-Weinberg equilibrium of single-locus genotype frequencies detected by the pV47-2 probe in burrowing owls.

	Source Population									
	All		Captive		Calif.		Davis		S. Clara	
	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Number of										
heterozygotes	67	77.5	9	8.2	58	66.5	52	58.4	6	7.1
homozygotes	20	9.5	1	1.8	19	10.5	15	8.6	4	2.9
P[a]	<.001		>0.5		<.01		<.05		>0.5	

[a] Based on the method of Chakraborty et al. (1991). Chi-square, 1 df; test results are given for homozygotes only; differences between observed and expected heterozygote frequencies are not statistically significant.

which uses the Chi-square distribution to test for an excess of homozygotes. I compared the observed proportions of homozygotes and heterozygotes of all types to those expected for a randomly breeding population at Hardy-Weinberg equilibrium. Table 2 summarizes these results for the combined samples (all groups) and for the successively smaller population units. This analysis suggests that the pool of all populations was genetically substructured, as was the collective California sample. Moreover, there was some evidence of nonrandom breeding, even in the Davis sample alone. The only groups that conformed to Hardy-Weinberg expectations were the samples from Santa Clara (which included one large sibship) and the captive-breeding project, both of which should exhibit Hardy-Weinberg ratios because they were limited to defined matings.

DISCUSSION

DNA fingerprints detected in the burrowing owl with the pV47-2 probe have single-locus, as well as multilocus, characteristics. This combination increases their value as markers for fine-scale population studies. Depending on the hybridization conditions used with DNA from this species, the pV47-2 probe alternatively has (1) the high resolving power typical of most minisatellite probes, or (2) the clear allelism and ease of scorability of a simple single locus with alleles characterized by a variable number of tandem repeats (see Gibbs et al. 1990). Similar cases of single locus probes loosely hybridizing at low stringency to alleles at many autosomal loci have been reported for birds (Gyllensten et al. 1989), as well as for other organisms (Higgs et al. 1986, Jarman et al. 1986, Nakamura et al. 1987, Ali and Wallace 1988, Fowler et al. 1988). Although the multilocus fingerprints of burrowing owls, like those described in the above studies, lack some precision in unambiguously resolving alleles because of some base-pair mismatch, the fingerprints are composed of highly variable Mendelian markers. Their major drawback, that DNA fragments cannot be attributed to particular loci, is offset by the ability, at the pV47-2 single locus, to analyze bands as traditional Mendelian, albeit hypervariable, alleles.

The use of DNA fingerprints as genetic population markers is also contingent on somatic stability and a relatively low rate of spontaneous gametic mutation. The estimated mutation rate per locus per generation for the burrowing owl (0.005) was within the range of values that have been reported for other birds, as well as for humans (0.003–0.05; Jeffreys et al. 1985a, Wetton et al. 1987, Rabenold et al. 1990), and would not invalidate use of the fingerprints for parentage determinations. Because the burrowing owl DNA came from red cells in peripheral blood, each sample represented an individual's entire erythropoietic system (see Longmire et al. 1988), indicating at least regionalized somatic stability.

Although I did not find significant deviation among the three burrowing owl population samples in fragment distribution or frequency, there is contradictory evidence for substructuring in the only wild population comprehensively sampled (i.e., Davis, California), based on the total number of homozygotes observed. That Hardy-Weinberg expectations were met in the Santa Clara and the captive breeding groups is hardly surprising, as such a small sample of parents virtually ensures Hardy-Weinberg equilibrium (i.e., the breeding system is reduced to just a few Mendelian crosses).

Nevertheless, these data suggest that selection is not acting to alter allelic frequencies at loci revealed in the DNA fingerprints.

If the data from the Davis sample can be generalized to other populations of burrowing owls, nonrandom breeding and subdivision may be occurring on very fine spatial scales (e.g., on the order of hundreds of meters). If the population is strongly subdivided, there may be elevated levels of inbreeding, and genetic effective population size may be small. In fact, estimates of relatedness based on DNA fingerprint similarity in the Davis burrowing owl population (see Johnson 1996b) indicate that the owls are experiencing inbreeding as a result of small deme size rather than nonrandom mating. In addition, if local populations are genetically and demographically isolated from one another, local extinctions may be exacerbated, and recolonization from extant populations may be less likely.

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REPRODUCTIVE SUCCESS, RELATEDNESS, AND MATING PATTERNS OF COLONIAL BURROWING OWLS

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ABSTRACT.—DNA fingerprinting was used to characterize patterns of mating, genealogies, and reproductive success in a wild population of burrowing owls (*Speotyto cunicularia*) in Davis, California. The data revealed important discrepancies between patterns suggested by inference and those documented by direct genetic measurement. DNA fingerprints showed that in 20% of the cases, genetically determined parent-offspring relationships and those suggested by direct behavioral observations disagreed. Differences were due to nestling movements and brood mixing, extra-pair fertilizations (which resulted in at least 5–10% of offspring), polygamy, and possibly intraspecific brood parasitism. These previously undocumented aspects of burrowing owl mating biology collectively resulted in alloparenting by 37% of the adult owls. Most of these behaviors can be expected to enhance within-population genetic heterogeneity and contribute to variation in individual reproductive success.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *DNA fingerprinting; extra-pair copulation; reproductive success; mating patterns.*

Exito reproductivo, parentesco y patrones de apareo de colonias del tecolotito enano

RESUMEN.—Huellas de ADN se usaron para caracterizar patrones de apareo, genealogia y exito reproductivo de poblaciones silvestres de tecolotito enano (*Speotyto cunicularia*) en Davis, California. Los datos mostraron importantes desacuerdos entre patrones sugeridos por inferencia y esos documentados por medidas geneticas directas. Huellas de ADN mostraron que en 20% de los casos determinados geneticamente y esos sugeridos por observaciones de conducta directa no estaban en acuerdo con respecto a parentescos padre-hijo. Las diferencias se debieron a movimiento de volantones y mezcla de nidadas, fertilizacion por otros individuos-no la pareja (que resultaron en cuando menos 5–10% de hijos), poligamia y posible parasitismo de nidada intraespecifico. Estos aspectos no documentados previamente de la biologia reproductiva del tecolotito enano collectivamente resultaron en allopadrazgo por 37% de tecolotes adultos. Se puede esperar que la mayoria de estas conductas realzen la hetorogeniedad genetica de la poblacion y contribuyan a la variacion en exito reproductivo individual.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) resembles most monogamous birds and most other owls in that both parents care for offspring. In other ways, however, it is unique. Although it is primarily a nocturnal predator, the burrowing owl is diurnally active, especially during the breeding season. It roosts and nests in subterranean burrows that are usually excavated by other animals, particularly mammals, that inhabit structurally simple grassland and desert habitats (Coulombe 1971, Martin 1973, Zarn 1974, Wedgwood 1976). Throughout extensive regions of its distribution, the burrowing owl nests in aggregations (often referred to as colonies), in part as a result of patchy dispersion of host burrows. In such instances, pairs can be densely distributed, numbering from several to tens in just a few hectares. At such densities, they are easily within visual range of each other during the months of breeding. Burrowing owl nestlings are brooded underground and emerge before they can fly. Even in this early prefledging stage (analogous to the "brancher" phase of arboreal owl development), the young owls range extensively on foot.

For other birds, high local densities and mobile young increase the risk that parents will care for foster offspring because they promote clandestine copulations with neighbors, egg-dumping by nearby females, and mixing or merging of broods

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(Gladstone 1979, Mock 1983, Westneat et al. 1990). Indirect behavioral evidence suggests that all of these behaviors are consequences of burrowing owl aggregation. For example, behavioral evidence for extra-pair copulations has been recorded for at least two other burrowing owl populations (Haug 1985, S. Honeyman and E. Musso, unpubl. data). In preliminary observations of color-marked burrowing owls, I saw attempts by both sexes to transfer care of offspring to individuals outside the pairbond. These behaviors included male solicitation of copulation with nearest-neighbor females and visits by females to burrows containing nests not their own. In addition, in each of two years, one nest in this burrowing owl population was defended and provisioned by three adults, further confounding my ability to infer parentage from behavioral observations and to determine relative reproductive contributions. Finally, brood mixing occurred regularly, making it difficult to estimate reproductive rates and intrasexual reproductive variance.

A number of recent studies that have used genetic tools to examine mating patterns and individual reproductive success in wild populations has confirmed that behavioral observations do not accurately reflect individual fitness in other social birds (Burke et al. 1989, Morton et al. 1990, Rabenold et al. 1990, Westneat et al. 1990). For this reason, I evaluated whether behavioral assessments of reproductive performance and mating system agreed with estimates obtained by genetic analysis for a highly social resident aggregation of burrowing owls. In addition, I sought to estimate the degree of genetic relatedness in this owl population in order to begin to understand genetic patterns that contribute to, and result from, burrowing owl group living.

METHODS

Study Population. I studied a wild population of burrowing owls in Davis, California, during four breeding seasons (April–September) in 1985–88. The population occupied remnants of nonnative annual grassland in a 150-ha human-dominated landscape, where the burrowing owls roosted and nested primarily in tunnels excavated by California ground squirrels (*Spermophilus beecheyi*). The site is on the campus of the University of California, Davis, where the presence of burrowing owls has been documented for at least the last 25 years (C. Barrows, L. Pompeli, and T. Schulz pers. comm.). The owls were somewhat habituated to humans, were relatively tolerant of ambient noise and human activity, and were readily observed with binoculars and a spotting scope. To minimize any disruption of naturally occurring owl behavior, I used a stationary vehicle as a blind and made behavioral observations from distances of between 50–200 m.

Color-marking and Behavioral Sampling. Population studies that focus on reproductive behavior require that individuals be unequivocally recognizable, so I color-banded as many owls as I could capture during the four breeding seasons of this study. I color-marked 112 burrowing owls, fitting every owl with a unique combination of four leg bands (two per leg). I recorded reproductive affiliations (mated pairs) and genealogies (putative parentage) of all burrowing owls, based on daily censusing and behavioral observations.

DNA Fingerprinting. I sampled blood from all burrowing owls captured in 1987–88. I used the minisatellite DNA probe pV47-2 (Longmire et al. 1990) to obtain DNA fingerprints from 67 of the Davis burrowing owls. I similarly analyzed DNA from 25 burrowing owls from other populations in California and Canada, including 2 captive families with known pedigree (see Johnson 1996). I compared these 'foreign' samples to those from the Davis population in order to calculate the genetic similarity of burrowing owls known to be unrelated. I excluded the 'foreign' samples from data sets used to characterize the wild Davis population.

Determination of Genetic Parentage. I combined several independent approaches in an attempt to determine the paternity and maternity of wild burrowing owls. I looked for concordance among four measurements, each of which has been used individually to ascertain genealogical relationships. These measurements included: (1) multilocus fingerprint similarity coefficients for offspring-parent pairs, (2) similarity coefficients for pairs of siblings, (3) presence of locus-specific offspring bands, and (4) attribution to parents of specific multilocus bands.

Similarity Coefficients. The similarity of DNA fingerprints can be used, within limits, as an index to the genetic relationship of two individuals and to average relatedness among members of a population (Lynch 1988, 1991). The most basic measure of similarity is the proportion of DNA fingerprint markers (bands) shared by any pair of individuals, and it is calculated from the equation $S = 2N_{XY}/(N_X + N_Y)$, where: N_{XY} is the number of DNA fragments common to the fingerprints of both individuals X and Y; N_X is the total number of fragments found in the profile of X; and N_Y is the total number of bands in Y. Coefficients of similarity (S-values) can theoretically range from 0–1.

To characterize the expected distributions of DNA fingerprint similarities for burrowing owls having different genetic relationships, I calculated S-values for pairs of individuals with known coefficients of relatedness (r). These comparisons were based on DNA fingerprints of owls from known pedigrees (see Johnson 1996). Their S-values should therefore approximate those for unrelated individuals in a randomly-breeding panmictic population. Two frequency distributions of similarity values were obtained for these samples, specifically, one for first-degree relatives ($r = 0.5$, $n = 18$ pairwise comparisons), including parents-offspring and siblings, and one for "non-relatives" ($r = 0$, $n = 27$), which was based on comparisons of all adults, non-siblings, and adults with offspring that were not their own. Similarity coefficients for pairs of close relatives ($r = 0.5$) averaged 0.6280. In contrast, the mean value of S-coefficients for presumed nonrelatives was 0.2812. I subsequently used these background similarity values to evaluate wild burrowing owl parentage and within-population relatedness.

RESULTS

Parentage of Offspring. I was able to propose putative parent-offspring relationships for 44 young owls, based on presence and behavior of adults at nests. Functional parents were confirmed as the actual parents of approximately 80% of the young owls. However, for nine other offspring (20.5%), one or both of the functional parents could not have been the true parent(s). The data also revealed at least two unambiguous extra-pair fertilizations, together accounting for at least two of 31 progeny (6.5%) that were produced and sampled in 1988. A third such case may have occurred in 1988. If three extra-pair fertilizations did occur, then approximately 10% (or more) of the 1988 cohort resulted from copulations extraneous to pair-bonds. During the two years of genetic study (1987 and 1988), two of the 20 breeding territories were occupied by three adult burrowing owls. In both of these trios, each of the adults was a parent of at least some of the offspring. Four other offspring were reared by pairs of adults, neither of which was their true parent. Instead, these progeny were produced by other mated pairs, including two nearest neighbors and two second-nearest neighbors. I suspect that exploratory movement by preindependent juveniles was the reason for genetic parentage being attributed to other mated pairs. In total, within one month of emerging, at least 20% of the young burrowing owls no longer associated with the nest at which they hatched, but with another nest.

Putative Versus Actual Reproductive Success. For many adults, the DNA fingerprints sampled during the two years of genetic study revealed differences between the number of young that were actually their offspring and the number inferred from behavioral observations. A difference in the number of actual and putative offspring occurred in 19 of 42 (45.2%) parent-brood combinations. There were more discrepancies in 1988 (68.4%) than in 1987 (26.1%). In both years, 12 of the 32 adults (37.5%) participated in rearing young that were not their own.

Population Similarity and Relatedness. DNA fingerprint similarity coefficients averaged 0.3358 for wild adult burrowing owls in the Davis population. This estimate was based on 48 separate within-gel comparisons of adults, exclusive of mates. The average coefficient of similarity for random adults in the Davis population was not only higher than that for known nonrelatives in the pedigreed captive families (0.2812; see Johnson 1996) but was also higher than the average fingerprint similarity calculated from presumably panmictic comparisons (0.2768).

I examined, in more detail, explanations for the relatively high mean similarity among owls in the Davis population. To estimate the incidence of mating by close relatives in the Davis population, I derived the mean similarity of DNA fingerprints from mated burrowing owls, 0.3309, based on 11 within-gel sample comparisons, and compared this value to the mean degree of similarity in the Davis population at large, 0.3358. Surprisingly, the DNA profiles of members of the mated pairs were slightly less similar to one another than were those of unmated adult burrowing owls in the population.

CONCLUSION

Although the identities of true parents of burrowing owl offspring often agreed with parent-offspring relationships indicated by behavioral observations, a substantial proportion (20%) of the field-based inferences were wrong due to extra-pair fertilizations, joint nesting, brood mixing and coalescence, and possibly intraspecific nest parasitism. These previously undocumented aspects of burrowing owl mating biology collectively resulted in alloparenting by at least 37% of the adult owls. In addition, owls in this population apparently bred nonassortatively with respect to the local pool of adults. Most of these behaviors can be expected to enhance within-population genetic heterogeneity and contribute to variation in individual reproductive success. However, the Davis burrowing owl population exhibited a higher mean coefficient of genetic similarity than did a collection of geographically separated owl populations, suggesting that some inbreeding is occurring in this wild owl population, probably as a result of small deme size due to population subdivision. Because inbreeding enhances selection between groups at the expense of opposing selection within groups, it can be expected to counter the effects of brood mixing and unequal reproductive contributions, and facilitate the evolution of burrowing owl social behavior.

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REPRODUCTIVE PERFORMANCE OF BURROWING OWLS (*SPEOTYTO CUNICULARIA*): EFFECTS OF SUPPLEMENTAL FOOD

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ABSTRACT.—The role of food in limiting the number of offspring fledged from nests (reproductive output) was experimentally investigated in a migratory population of burrowing owls (*Speotyto cunicularia*) in Saskatchewan, Canada. Dead laboratory mice were provided to 12 of 26 owl pairs during egg laying in 1992. Food-supplemented owls laid slightly larger clutches and produced eggs of higher volume, but did not show higher hatching success or produce more hatchlings than did unsupplemented birds. Pairs that were supplemented during the nestling stage only ($N = 8$) exhibited less cannibalism and fledged more young than did unsupplemented pairs ($N = 11$). These preliminary results suggested that, although food intake restricted the number of eggs that burrowing owls laid, the total number of young produced at a nest was constrained by food only during the nestling period. Food intake was thus more limiting during brood rearing than during egg laying.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *food limitation; food supplementation; clutch size; egg volume; cannibalism; nestling stage.*

Desempeño reproductivo del tecolotito enano (*Speotyto cunicularia*): efectos de alimentacion suplementaria

RESUMEN.—El papel del alimento como limitante de crias volantones de los nidos (rendimiento productivo) se investigo experimentalmente en una poblacion migratoria de tecolotito enano (*Speotyto cunicularia*) en Sakatchewan, Canada. Ratones de laboratorio muertos se dieron a 12 de 26 pares de tecolotes durante el periodo de la puesta de huevos en 1992. Los tecolotes con alimentacion suplementaria pusieron mas huevos y produjeron huevos de mayor volumen, pero no mostraron mayor exito de empollo o produjeron mas pollos que las aves sin alimentacion suplementaria. Parejas que se suplementaron durante el periodo de cria solo (N = 8) mostraron menos canibalism y tuvieron mas jovenes volantones que las parejas sin suplementacion (N = 11). Estos resultados preliminares sugieren que a pesar de que el consumo de alimentos restringio el numero de huevos puestos por los tecolotitos enanos, el numero de juveniles producidos por nido estaba restringido unicamente por alimento durante el periodo de cria. El alimento entonces fue mas limitante durante la cria de la nidada que durante la puesta de huevos.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) has been designated an Endangered species in Canada (Wedgwood 1978, Wellicome and Haug 1995) because of an alarming decline in its population (James and Fox 1987, Haug and Oliphant 1990, Haug et al. in press). The decrease in habitat quality and availability that has resulted from the steady increase in agricultural and urban development is believed to be the factor ultimately responsible for this decline (Zarn 1974, Wedgwood 1978, Haug and Oliphant 1990, Schmutz et al. 1991, Haug et al. in press); however, proximate factors have yet to be identified (Wedgwood 1978, Haug 1985, James and Fox 1987).

Proximate factors can cause population declines by reducing either recruitment (the number of first-time breeders) or survival, or both (Temple 1986). Unfortunately, studying survival rates of Canada's burrowing owls is difficult because they spend half of each year wintering in unknown areas at least as far south as Mexico (James 1992), and their degree of nest-site fidelity has not been

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well documented (Schmutz et al. 1989). Therefore, at present, the most feasible approach for addressing the population decline in Canada is to identify factors on the breeding grounds that affect recruitment.

Food limitation in birds is a common problem resulting from human-caused habitat alteration (Temple 1986). Previous authors have suggested that natural food supply may constrain reproduction in burrowing owls. Butts (1973) proposed that availability of vertebrate prey in the spring limited the reproductive output of owls in Oklahoma. Gleason (1978) showed that brood size increased with proximity to irrigated agricultural areas in Idaho, implicating prey availability as the causal factor. However, these studies provide only circumstantial evidence to support the hypothesis that food limits reproduction. In this study, I investigated the effects of food intake on reproductive output (one component of recruitment) by manipulating the amount of food available to breeding burrowing owls.

The two periods of the breeding season most commonly thought to represent energetic "bottlenecks" for birds are the egg-laying and brood-rearing stages (Martin 1987, Arnold 1992). Separate food supplementation experiments were conducted during each of these two periods.

METHODS

Burrowing owls were studied in the Grassland Ecoregion of Saskatchewan (Harris et al. 1983) from mid-April to mid-August, 1992, on a site situated south of the cities of Moose Jaw and Regina. The majority of the study area lies on the Regina Plain with the southernmost portion extending into the Missouri Coteau. Intensive cultivation in this region has left a heavily-fragmented landscape (James et al. 1990). Consequently, most owls nest in small, heavily-grazed pastures that are interspersed among a variety of habitat types, including cereal crops, summer fallow, hayland, and other grassland.

In May, one to two weeks after each pair had chosen a burrow and began lining its entrance with nesting material, a wooden artificial nest burrow (ANB) was installed within the natural burrow. This method of ANB introduction yielded a nest-use success rate of 94% (17 of 18 burrows; see also Olenick 1990). An additional 11 pairs prepared nests in wooden ANBs that had been in place prior to 1992, for a total of 29 occupied boxes. ANBs enabled me to count and measure eggs, establish laying and hatching dates, and monitor chick mortality. Pellets were collected near nests, roost burrows, and favorite perches at 3-d intervals throughout the breeding season.

Supplementation During Egg Laying. Because disturbance in the nest chamber during early laying is thought to increase the frequency of nest abandonment (Olenick 1990), I used evidence from aboveground observations to estimate clutch-initiation date. Laying was considered to commence when a female began spending most of her time inside the nest burrow.

Since food supplementation often leads to earlier laying (Arcese and Smith 1988) and earlier clutches are typically larger (Nilsson and Svensson 1993), it is important to experimentally separate laying date and clutch size (Nilsson 1991) if effects on clutch size are to be directly attributed to food intake. Hence, pairs were ranked by their estimated date of laying and then alternately assigned to supplemented and unsupplemented groups to remove effects of initiation date. Actual initiation dates were later determined by backdating from egg counts conducted prior to clutch completion (one egg is laid every 36 hr; Olenick 1990). Actual laying dates were, on average, 2.7 d after estimated laying dates (range: 6 d after to 3 d before). Nonetheless, the distributions of actual laying dates did not differ between experimental and control pairs (mean Julian date [SE]: 128.4 [0.9] vs. 130.5 [1.1], respectively; Kolmogorov-Smirnov two-sample test, $P = 0.34$, two-tailed).

Each of fourteen pairs was provided with dead white laboratory mice at 3-d intervals, beginning on the estimated day of clutch initiation (mean Julian date [SE]: 125.7 [1.0]). Supplementation continued through egg laying unless the nest attempt failed. Pairs were provided with food at a rate of approximately 65 g/nest/d, corresponding to more than twice the daily existence metabolism of an adult burrowing owl in captivity (mean = 26 g; Marti 1973). Fifteen control (unfed) pairs nesting in ANBs were visited every third day and disturbed for the same amount of time as were supplemented pairs.

The proportion of white fur in a randomly chosen subset of collected pellets (143 pellets from 21 visits) was estimated visually to give a rough measure of the proportion of supplemental food in the diets of supplemented owls. White fur from laboratory mice was easily distinguished from light-colored fur of other small mammals.

Clutch sizes were determined by counting eggs shortly after clutch completion. Egg dimensions were measured to the nearest 0.01 mm with dial calipers, and egg volumes were calculated using Hoyt's (1979) equation: $V = 0.000507*L*B^2$ (where V = volume, L = maximum length, and B = maximum breadth). Egg-size comparisons were based on mean egg volume per clutch.

Supplementation During Brood Rearing. Each of five unfed pairs from the above experiment were supplemented with food every third day for 40 d, beginning at the date of first hatch (mean Julian date [SE]: 160.4 [1.0]). Four additional pairs nesting in natural burrows (where hatch date and initial brood size could not be determined), were fed during this same time period (mean Julian date of first feeding [SE]: 160.7 [0.7]). Food was provided at a rate of 65 g/nest/d early in brood rearing and was increased to 75 g/nest/d late in the nestling stage. Four of the control pairs from the first experiment (see above) nesting in ANBs and ten previously undisturbed pairs nesting in natural burrows served as controls during the nestling period. Nest contents in ANBs were checked every third day during feeding or control visits. Both tarsi on each nestling were color-

Table 1. Clutch size, egg volume, hatching success, and number of hatchlings for burrowing owl pairs supplemented with food during egg laying and for control pairs. Fledging success and number of fledglings for owls supplemented during brood rearing and for control owls.

	Treatment						Difference[a]	
	Supplemented			Unsupplemented				
Parameter	$\bar{x} \pm$ SE	Median	N	$\bar{x} \pm$ SE	Median	N	U	P
Egg laying								
Clutch size	9.3 ± 0.2	9.5	12	8.9 ± 0.2	9.0	14	110.0	0.08
Egg volume (cm^3)	11.29 ± 0.22	11.19	12	10.89 ± 0.11	10.90	13	105.4	0.07
Hatching success (%)	90.2 ± 2.8	90.0	11	83.8 ± 5.6	90.0	11	65.0	0.38
No. hatchlings	8.4 ± 0.3	9.0	11	7.6 ± 0.6	8.0	11	73.0	0.20
Brood rearing								
Fledging success (%)	100.0 ± 0.0	100.0	5	81.0 ± 8.7	17.5	4	17.5	0.01
No. fledglings[b]	7.3 ± 0.4	7.5	8	6.2 ± 0.3	6.0	11	66.0	0.03

[a] One-tailed Mann-Whitney U-tests.
[b] Fledglings from both artificial and natural burrows.

marked using felt pens, allowing individual identification. When tarsus width reached its maximum, nestlings were fitted with aluminum bands. Natural burrows were observed for 30-min bouts on three or more occasions late in the nestling period to determine the number of nestlings fledged. A nestling was considered to have fledged if it was observed at a nest or satellite burrow 40 d or more after hatch. The age of young at natural burrows was estimated by comparing their morphologic measures or levels of feather development to known-age young from ANBs.

To ensure that fed and unfed groups had similar initial brood sizes, nests were ranked by clutch size and then alternately assigned to each treatment. As a result, the distribution of initial brood sizes (range: 6–10 hatchlings) did not differ between fed and unfed treatments (mean [SE]: 7.4 [0.6], N = 5, vs. 8.3 [0.9], N = 4, respectively; Kolmogorov-Smirnov two-sample test, P = 0.98, two-tailed). This method of assigning pairs could only be performed when clutch sizes were known, so pairs in natural burrows were assigned to each treatment at random.

In birds of prey, cannibalism often results from food stress (Bortolotti et al. 1991). In the present study, cannibalism was defined as the consumption of the flesh of a conspecific, regardless of how death occurred, following Bortolotti et al. (1991). A mortality was considered to be cannibalism if the remains of a nestling (i.e., feathers, bones, or an aluminum band) were observed in an ANB, or if, early in the nestling period, a chick disappeared between successive nest checks (3-d intervals; Bortolotti et al. 1991).

Statistical Analyses. All statistical tests were performed using SYSTAT for Windows (Wilkinson 1992). To lower the probability of committing a type-II error due to small sample sizes, a type-I error probability of 0.10 was *a priori* deemed as acceptable for significance testing (Krebs 1989). Egg volume, % of eggs hatched, number of hatchlings produced, % of nestlings surviving, and number of young fledged were compared between fed and unfed treatments using Mann-Whitney U-tests. Student's t-tests were not used because small sample sizes precluded accurate testing of normality and homogeneity of variances. One-tailed tests were used because effects in only one direction are meaningful to the hypotheses tested (Sokal and Rohlf 1981, Korpimäki 1989, Simons and Martin 1990). Incidence of cannibalism was compared between treatments using a G-test for independence with 1000 random iterations.

RESULTS

Egg Laying and Incubation. Of the 29 pairs that initiated laying, three failed prior to clutch completion and therefore could not be included in the experiment. Two of these (one fed and one unfed) abandoned their nests after laying five eggs each. Also, one male from a food-supplemented pair was killed by a Swainson's hawk (*Buteo swainsoni*). The other 26 owl pairs completed and incubated their clutches.

White fur from laboratory mice constituted an average of 27% of the volume of analyzed pellets from experimental nests during egg laying. No white fur was found in the pellets of unsupplemented owls.

Females given extra food produced an average of 0.4 more eggs than did controls, representing a 4.5% increase in clutch size (Table 1). In addition, the eggs of fed pairs were larger than those of control pairs, averaging 0.4 cm^3 (3.7%) greater in volume.

Four nesting attempts failed late in the incubation stage: two pairs abandoned (one had been fed during egg laying and one had not), one pair deserted because of human disturbance, and one clutch (unfed) was depredated.

There was no difference in hatching success between birds that had been fed during egg laying and those that had not (Table 1). The total number of hatchlings in nests that had received extra food did not differ from that in nests that had not received extra food. Thus, the larger clutches and eggs of supplemented pairs did not result in larger broods, and therefore food addition during egg laying did not ultimately increase reproductive output.

Brood Rearing. Of the 23 broods used in the nestling-supplementation experiment, four failed to fledge any nestlings. One of nine (11%) supplemented broods and three of 14 (21%) unsupplemented broods were lost to predators.

Analysis of a 121-pellet subset collected during 20 separate visits to experimental nests during brood rearing showed that white fur composed 24% of the volume of pellets.

Survival of owlets was monitored at nine ANBs throughout the nestling period. Incidence of cannibalism was higher for unsupplemented broods (3 of 4 ANBs) than for supplemented broods (0 of 5 ANBs; G-test for independence, $G_{ran} = 6.96$, $P = 0.03$), resulting in a lower proportion of young being fledged by unfed pairs than by fed pairs (Table 1). Feathers, bones, and bands of cannibalized nestlings were found in pellets of both siblings and parents, and beheaded nestlings were sometimes found in caches with other prey. In every case, the victim was the smallest of nestlings remaining in the brood (TIW unpubl. data).

Supplemented pairs fledged between six and nine young from ANBs and between six and eight young from natural burrows. Unsupplemented pairs fledged between five and eight young whether nesting in ANBs or natural burrows. When natural and artificial burrows were considered together, supplemented pairs fledged significantly more young than did controls (Table 1). Fed pairs produced an average of 1.1 (17.3%) more fledglings than did unfed pairs.

DISCUSSION

The reproductive output of burrowing owls appears to be limited by food intake. Food-supplemented pairs produced slightly larger eggs and clutches, had a lower incidence of cannibalism, and produced more fledglings than did unsupplemented pairs. Because food supplementation was conducted at different stages of the reproductive cycle (as suggested by Hochachka and Boag 1987), I was able to determine that food intake was more limiting during brood rearing than during egg laying. These experiments were replicated in 1993 with larger sample sizes. Results from 1993 appear to agree with those from 1992 experiments, but the data have not yet been fully analyzed.

Food intake at the nest may be limited for many reasons: (1) habitat quality limits prey abundance or prey availability, (2) foraging areas are far from nesting areas, so energy costs of transporting prey are high, (3) weather limits the number of hunting hours or modifies the behavior of prey, making them less available. The third factor is beyond the control of management, but the first two potential limitations can be alleviated through habitat improvement: habitats that support abundant, available prey in the vicinity of active owl nests could be recreated or enhanced. Prey monitoring during the season and observation of habitat use by foraging owls would determine which habitat types would be most profitable to improve.

It may be common for birds of prey to be reproductively limited by food (Martin 1987, Newton 1989). Experimental food addition has resulted in increased fecundity in a number of species of raptors: Eurasian sparrowhawk (*Accipiter nisus*) (Newton and Marquiss 1981), Eurasian kestrel (*Falco tinnunculus*) (Dijkstra et al. 1982), and Tengmalm's owl (*Aegolius funereus*) (Korpimäki 1989, Hornfeldt and Eklund 1990). The increase in clutch sizes of Eurasian sparrowhawks with supplemental feeding occurred in poor-quality habitat (Newton and Marquiss 1981). Intensive land-use practices (cultivation for cereal crops and heavy grazing of prairie for cattle production) may have reduced the quality of burrowing owl habitat on much of the Canadian prairies by reducing the availability of natural prey. This would explain the response of burrowing owls in southern Saskatchewan to extra food. Owls nesting in Alberta in an area with restricted cultivation (15% of land area) and moderate grazing pressure, show higher reproductive output and are declining more slowly (Schmutz et al. 1991) than are owls in Manitoba and Saskatchewan (Haug et al. 1995). Schmutz et al. (1991) attribute these differences in breeding success to differences in natural prey supply among the areas. Supplementation studies conducted also in areas of low-intensity agricultural land use could substantiate this assertion.

For species such as the burrowing owl that are declining in numbers precipitously, it is desirable to promptly stabilize populations by slowing or halting their decline until ultimate causes can be identified and, if possible, corrected (Temple 1986). Food supplementation is a short-term management technique that will immediately increase burrowing owl reproductive output where prey supply is limiting. Feeding can be restricted to the nestling period, when additional food appears to have the greatest benefits. Over the long term, it may be worthwhile to increase prey supply through habitat restoration in the vicinity of nests.

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REPRODUCTIVE ECOLOGY OF THE BURROWING OWLS, *SPEOTYTO CUNICULARIA FLORIDANA*, IN DADE AND BROWARD COUNTIES, FLORIDA

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Abstract.—From 1988–90 a study of the reproductive ecology of the burrowing owl (*Speotyto cunicularia floridana*) was conducted to determine breeding chronology and success in Dade and Broward Counties. Reproductive data for each of the three years revealed a higher percent of successful territories (54%) for 1990 than for 1989 (40%) and 1988 (41%). Owls occupying previously established burrows had a higher success in fledging young (63%) than those using newly excavated burrows (19%). Flooding was the primary cause (63%) for nesting failures. Car collisions accounted for 50% of known mortalities.

Key Words: *burrowing owl;* Speotyto cunicularia floridana; *reproduction; Florida.*

Ecologia reproductiva del tecolotito enano, *Speotyto cunicularia floridana* en los Condados Dade y Broward, Florida

Resumen.—De 1988 a 1990 un estudio de la ecologia reproductiva del tecolotito enano se realizo para determinar el exito de la chronologia reproductiva en los condados Dade y Broward. Datos reproductivos para cada uno de los 3 años (1988–1990) muestran una tasa de reproduccion mas alta (54%) en 1990 que en 1989 (40%) y 1988 (40%). Los tecolotes que ocupaban madrigueras previamente establecidas tuvieron exito reproductivo mas alto de pollos volantones (63%) que aquellos que usaron madrigueras recian excavadas (19%). Inundacion fue la causa principal de fracasos en anidicaion. Colisiones con autos fueron la causa de 50% de la mortalidad conocida.

[Traducción de Filepe Chavez-Ramirez]

Burrowing owls, (*Speotyto cunicularia*), are small crepuscular owls found throughout North America, the West Indies (Cory 1891, Howell 1932), portions of Central America (Land 1970) and the western coast of South America (Jaksić and Marti 1981). In continental North America there are two subspecies. The western burrowing owl, (*S.c. hypugaea*), resides in the dry grasslands, prairies and farmlands (Coulombe 1971) of western North America. The Florida burrowing owl, (*S.c. floridana*), lives primarily in naturally occurring high sandy ground of central, eastern, and western Florida (Rhoads 1892, Bent 1961), pastures (Ligon 1963), airports (Owre 1978), as well as vacant and residential lots (Wesemann 1986).

Burrowing owls in Florida are presently expanding from their former range (Neill 1954). The burrowing owl was first recorded in Florida by N.B. Moore in 1874 (Courser 1979). Historically, this owl reproduced primarily in the central portion of the peninsula (Sprunt 1954). Large expanses of native wooded areas have been cleared with the augmentation of development, dairy production and agriculture (Tebeau 1971). Land clearing and supplemental fill have provided more habitat for the burrowing owl in Florida (Betz 1932, Ligon 1963, Garrido and Montana 1975, and Courser 1979).

In southern Florida, Dade and Broward Counties, burrowing owls have established nesting territories in airports, pastures, sports fields, golf courses, university and college campuses, parking lots, roadway medians and in the yards of private residences. Remaining pastures in Broward County are under extreme demand from development. To survive, the dairy industry has had to increase cattle densities to augment productivity. The higher number of cattle has increased contacts with the owls resulting in a higher number of destroyed burrows.

The burrowing owls' ability to successfully adapt to altered habitats is limited. The degree of development within a given site may determine the future success of these small raptors. The Nongame

Wildlife Program of the Florida Game and Fresh Water Fish Commission (FGFWFC) and the Audubon Society of Southwest Florida are correlating the percent cover of development within their study sites and the burrowing owls' ability to successfully fledge young. In the first three years of their study, 1987–89, they observed a decline in fledgling production when the development exceeded 75% of an area. Even though these owls have the ability to tolerate human intrusion, the decline of suitable nesting habitats may be their limiting factor (Wesemann 1986, Millsap 1988).

The purpose of this project was to document the reproduction and general ecology of the burrowing owl at three different study sites in Dade and Broward Counties between December 1987 and September 1990.

STUDY AREA AND METHODS

Study Sites. Three sites were chosen for this project: the Miami International Airport (Dade County), a dairy farm (Imagination Farms) and private residences (southwestern Broward County). Approval from all owners was given prior to working on their property.

MIA is located in western Dade County, has three runways on 1293 ha, 70% of which is developed and paved. There is continuing pressure for runway and terminal expansion to accommodate the increased flow of air traffic. The burrowing owls' territories are in the sandy medians between the runways, taxiways and the inner perimeter road. Most territories are located adjacent to the inner perimeter road. The second study site is Imagination Farms, Inc. in the southwest corner of Broward County in the town of Davie. It is a dairy farm covering 240 ha. The third study site contains five separate areas located in several residential developments and estates in southwestern Broward County: the town of Davie, Rolling Oaks, Sunshine Ranches Estates, the Rock Creek Residences in Cooper City, and Ivanhoe Estates.

Locating Owls. Burrowing owls were located while driving a vehicle on roads, through pastures and along the airport's roadways. The birds were located by looking for their bobbing motion (Thomsen 1971) or by locating the highly exposed sandy mounds at the entrance of their burrows. Active burrows had evidence of excavated soil and a clear unobstructed entrance. Decorated entrances identified the nesting burrows of a territory. Inactive burrows were usually obstructed with grass or weeds, and most had spider webs. Once the territories were well established the owls became highly visible.

Owl Identification. The burrowing owls were individually identified with a numbered USFWS aluminum band on one leg and a plastic numbered color band (Gey Band and Tag Co.) on the opposite leg.

Capture Techniques. The owls were caught using a variety of methods. The most successful technique was the use of a noose carpet attached to a 180 g weight placed at the entrance and perimeter of the burrow (Kahn and Millsap 1978, Bloom 1987). Bal-chatri traps were used on several occasions (Berger and Mueller 1959, Beebe and Webster 1976) with infrequent success. The final method involved approaching the burrow from the blind side and capturing the owls by hand by reaching down the burrow. This method proved most successful in catching young owls at the airport and residences. The noose carpet was most effective when the owls excavated or continuously moved around at the entrance of the burrows. Once captured, the owls were immediately wrapped in a cloth to act as a hood. This handling technique prevented injuries from tongue-snapping, a stress induced response. If a cloth was not readily available, the mandibles were held closed with fingers. While wrapped in the cloth, the owls were promptly banded in the event of an early escape.

An owl census was conducted weekly at each territory in all of the study sites. The census involved recording the total number of owls observed, the number of adults present, the total number of young, the total number of fledged young, and the number of banded owls. Census was conducted during the owls' breeding period, January–August.

Breeding Chronology. Breeding chronology was determined by the number of owls observed during weekly visits to the study sites. No attempts were made to differentiate between the young and adult owls for the chronology data. The highest weekly count of owls in a given month was used to plot the graph. The seasonality data were plotted with pooled data for each of the study sites. Productivity was determined by observing young outside the burrow and counting the number that successfully fledged from a territory. A territory was considered successful if one or more young fledged from it (Steenhof 1987). Mean values in results are followed by ± two standard errors. In 1988, field inexperience may have accounted for an overestimate in the number of territories observed in the study sites. Several pairs had satellite burrows (Thomsen 1971, Wesemann 1986) at distances of over 30 m that may have been mistaken for additional territories. The territories observed in 1989 and 1990 were closely scrutinized to minimize this potential error.

Data were analyzed by using statistical methods described in Sokal and Rohlf (1981) and with AbStat (copyright, Anderson-Bell Co. 1984) and Ecological Analysis (Eckblad 1986) statistical software packages.

RESULTS

Chronology. Three years of data show a late spring peak in burrowing owl numbers in all of the study sites (Fig. 1). Owls appeared in January, and sightings rapidly increased until about the month of June. Numbers peaked in late May and early June. During the following months, the sightings decreased as adults shifted to a more crepuscular and nocturnal behavior and the young dispersed to new areas. The onset of summer and the rainy season probably play major roles in the shift in behavior and in fledgling dispersal due to the flooding of burrows.

Productivity. Reproductive data for each of the years (1988–90) reveals a higher success rate

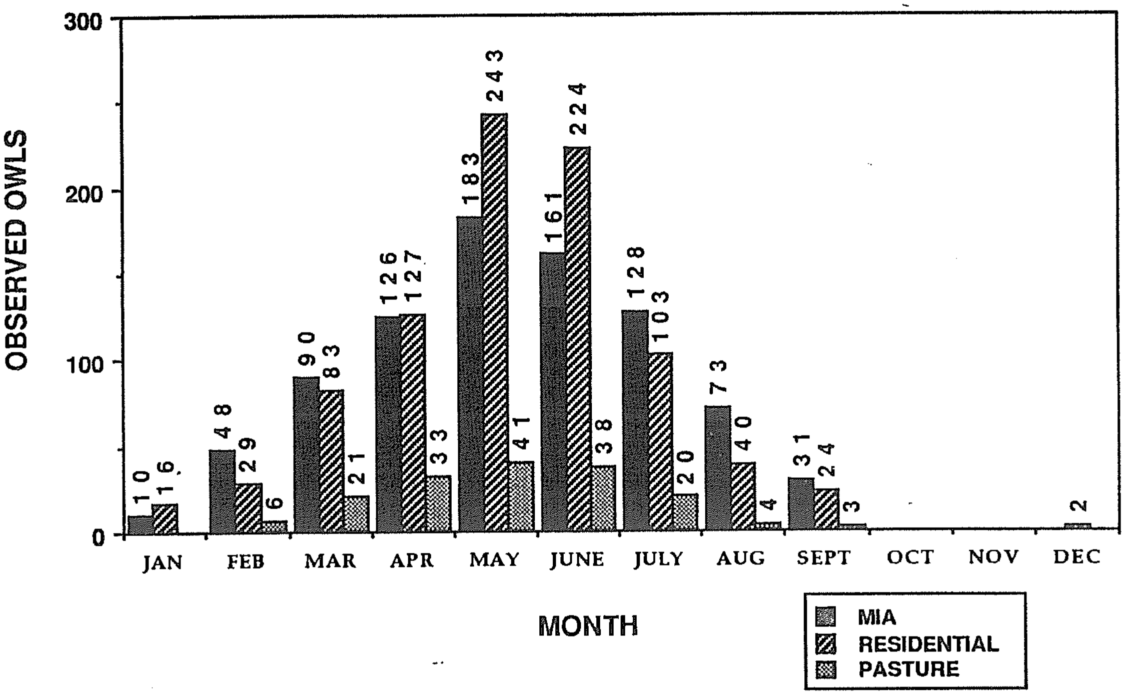

Figure 1. Number of burrowing owls observed by month during 1988–90.

(54%) for the 1990 season than the 1988 (41%) and 1989 (40%) seasons (Table 1). The pastures were the only study site that showed a relatively lower percent of successful territories in 1990 (14%, Table 2). This decrease is probably due to the increased cattle density and the infrequent mowing schedule that caused the vegetation to grow over the opening of the burrow. In 1990, the MIA and the residences both showed the highest percent in the number of successful territories (58%) and in the mean value of young fledging, at MIA $\bar{x}$ = 2.42 ± 0.5 and at the residences $\bar{x}$ = 2.84 ± 0.46 (Table 2).

The residential sites are an array of estates located in southwest Broward County. I added two additional study sites, Sunshine Ranches and Ivanhoe Estates in 1989–90, to the three study sites in 1988. From 1988–90 all residential study sites had an increase in the number of territories (Table 2). Except for Davie, all study sites also had an increase in the percent of successful territories.

Nest Decoration. Burrows were often decorated with a variety of materials found within or outside the boundaries of the territory. This included animal fecal material, aluminum foil, paper, string, other trash, and animal parts. Decorated burrows were a sign of occupied territories. Data suggested no relationship between decoration and nesting success. From 164 decorated territories, 84 (51%) fledged young and 80 (49%) failed. The use of

Table 1. Reproductive analysis for all territories from 1988–90 ±2 standard errors.

Year	No. of Territories	No. of Successful Territories	% of Successful Territories	$\bar{x}$ Young All Territories	$\bar{x}$ Fledged All Territories
1990	79	43	54%	2.80 ± .32	2.73 ± .34
1989	75	30	40%	2.46 ± .38	2.46 ± .38
1988	66	27	41%	2.56 ± .44	2.37 ± .40

Table 2. Burrowing owl reproductive data (±2 standard errors) from three study sites from 1988–90.

Study Site	No. of Territories	No. of Successful Territories	% of Successful Territories	$\bar{x}$ Young All Territories	$\bar{x}$ Fledged All Territories
1990					
Miami Int'l. Airport	24	14	58%	2.50 ± .5	2.42 ± .5
Residential	48	28	58%	2.90 ± .44	2.84 ± .46
Pastures	7	1	14%	4.00 ± 0	4.00 ± 0
1989					
Miami Int'l. Airport	27	12	44%	2.16 ± .54	2.16 ± .54
Residential	42	16	38%	2.75 ± .56	2.75 ± .56
Pastures	6	2	33%	2.00 ± 0	2.00 ± 0
1988					
Miami Int'l. Airport	32	15	47%	2.46 ± .52	2.33 ± .54
Residential	20	8	40%	3.00 ± .74	2.75 ± .72
Pastures	14	4	29%	1.75 ± .94	1.75 ± .94

dung has been shown to have little value in increasing a pair's potential to fledge young in these study sites of southeast Florida. From 193 territories in which dung was used, 87 (45%) fledged young and 106 (55%) failed.

Burrow Reuse. During the three years of this study 60% of the burrows were reused from previous years with a higher percentage in reproductive success rate than newly excavated burrows. From 84 territories with burrow reuse, 53 (63%) territories successfully fledged at least one young, while in 47 territories with new burrows, only 9 (19%) of them fledged young.

Nesting Failures. Of 123 known failures only 33 (27%) had clearly attributable causes. The primary reason for known nesting failures was flooding (N = 21, 63%). Other causes were collapse due to cow trampling (N = 6, 18%), human activities (N = 4, 12%), and predation (N = 2, 6%).

Mortality. Mortality data are for banded and unbanded specimens found in the study sites. Of 18 owls, 9 (50%) were killed by cars, 4 (22%) by drowning, 2 (11%) due to burrow collapse, 2 (11%) by predation, and 1 (5%) by electrocution.

Discussion

The Florida burrowing owl is currently listed as a species of special concern by the FGFWFC. The owls become more prevalent in January at the onset of the breeding season and the numbers peak in late May and early June. The increase in numbers has also been observed in New Mexico (Martin 1973), where numbers also peak in late May and early June. During the following months, sightings begin to decrease as adults shift to a more crepuscular and nocturnal behavior (Thomsen 1971), and most of the young begin to disperse to new areas (Martin 1973).

In areas categorized as heavy development (i.e., 75% developed) by Millsap (1988) the populations began to decline. In 1988, 60% of nesting failures in Cape Coral were a direct result of human activities (Millsap 1988). Courser (1976) documented a population decline due to development in a similar area near Tampa, Florida.

Comparing overall fledgling rate per breeding pair in studies of the western burrowing owl, the Florida burrowing owl has a lower productivity. Thomsen (1971) and Martin (1973) report fledgling rates between 2.2–5.5 per breeding pair for the western burrowing owl, while Millsap (1988) and Mealey (this report) report fledgling rates of 1.59–2.75 for the Florida burrowing owl.

In Dade and Broward Counties the population appears to be expanding to areas of new development. In areas that are zoned for residences with 0.40 ha or more, preliminary results indicate a stable population. This could be due to a limited number of people and fenced-in yards that provide protection. The residential areas of this study with 0.40 ha or more include Ivanhoe Estates, Sunshine Ranches, Davie, and Rolling Oaks. The mortality factors include flooding, human intolerance, and use of home pesticides.

Preliminary banding results (Millsap 1988) show territory fidelity. Currently, nesting behavior is used to identify the sexes. Incubation is believed to be primarily conducted by the females. Males provide food and select the territory. Usually, if a pair disappears from its territory it is assumed that the male is dead (B.A. Millsap per. comm.). Land alteration and development has contributed to the increases in Florida's burrowing owl population but eventually may be the cause of its decline.

Unlike the western subspecies, which need the protection of the natural habitat and the burrowing mammal population (Green 1983), the survival of the Florida subspecies may depend on the proper education of residents in documented key residential breeding grounds and by limiting the degree of alteration in future development sites (Millsap 1987). Burrowing owl breeding success at MIA of 58% (1990) coincides with success rates in Oregon of 57% (1980) and 50% (1981) (Green 1983) and at the Oakland Municipal Airport in California of 54% (1971) (Thomsen 1971). The continuing existence of the burrowing owl population at the MIA will be closely tied to the amount of development that takes place to accommodate future air travel.

Burrowing owls can only temporarily halt a project. The FGFWFC and the U.S. Fish and Wildlife Service issue permits to take or destroy inactive burrows outside of the nesting season. On occasion a permit may be issued during the nesting season to destroy a nest after the young have fledged. Care must be taken not to issue permits prematurely during the nesting season. Even though young may be defined as fledged they are still dependent on the primary and satellite burrows for a period of 30–60 days after they start flying.

Since land development is one of the primary causes for the owls' decline, improved and aggressive management strategies should be implemented to decrease known mortalities within successful breeding habitats. Simple requirements such as speed limit signs in conjunction with speed bumps would significantly decrease vehicle-related mortalities. Tax incentives should be awarded to contractors who voluntarily incorporate wildlife management and habitat restoration protocols into large development plans. Species coexistence and survival will depend on federal and state wildlife agencies to develop strict and enforceable guidelines/policies on future development projects.

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SELECTED MICROHABITAT VARIABLES NEAR NESTS OF BURROWING OWLS COMPARED TO UNOCCUPIED SITES IN ALBERTA

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ABSTRACT.—to examine the possibility that there may be more suitable nesting habitat in a grassland area of Alberta than burrowing owl (*Speotyto cunicularia*) pairs to fill it, I compared habitat parameters between nesting areas and systematically matched unoccupied grassland sites. There were no statistically significant differences in the density of grasshoppers, the number of American badger (*Taxidea taxus*) or ground squirrel (*Spermophilus* spp.) burrows, or the extent of cultivation. Although it is possible that one or more of the many factors not examined here limit owl numbers on the study area, it is also possible that factors operating on migration or in winter may limit survival of this threatened owl below carrying capacity.

KEY WORDS: *burrowing owl*; Speotyto cunicularia; *habitat*; *Canada*; *Alberta*; *prey*; *nesting*; *burrows*.

Variables de microhabitat seleccionadas cerca de nidos de tecolotito enano comparadas con sitios desocupados en Alberta.

RESUMEN.—Para examinar la posibilidad de que hay mas lugares adecuados para habitat de anidacion en areas pastizales de Alberta, que parejas de tecolotitos enanos para ocuparlos, compare parametros del habitat entre areas de anidacion con areas sistematicamente matched con sitios de pastizal desocupados. No se encontraron diferencias significantes en la densidad de chapulines, el numero de madrigueras de tejon (*Taxidea taxus*) y ardillon (*Spermophilus* spp.), o el grado de cultivacion. Aunque es posible que uno o mas de los factores no examinados aqui puedan limitar el numero de tecolotes en el area de estudio, tambien es posible que factores que operan en migracion o en areas invernales puedan limitar sobrevivencia de este tecolote amenazado que se encuentra bajo el limite de capacidad de carga.

[Traducción de Filepe Chavez-Ramirez]

Identifying the relative importance of factors that may influence the dynamics of "threatened" burrowing owl (*Speotyto cunicularia*) populations in Canada has proven difficult. The present study was sparked, among other observations, by reports from local landowners that burrowing owls have declined in recent decades in the absence of obvious changes in habitat or land use. This study was carried out in one of the least altered grasslands of Canada. Here, some native range remains, farmland long since abandoned has been revegetated (Dormaar and Smoliak 1985), and a ranching land use is regulated by the municipal government (Gorman 1988). Despite what superficially appears to be ample grassland suitable for burrowing owls, the density of owls recorded in a survey of 67 km^2 of land was 19.5 nests/100 km^2 (Schmutz 1993).

In this study I compared selected habitat and food variables around burrowing owl nests with systematically matched sites 1 km away. If no difference was discernible between nests and unoccupied sites, this might be consistent with the conclusion that more habitat is available than is presently occupied by the owls. I chose to measure grasshopper abundance because insects including grasshoppers are an important food source for owls in the population studied (Schmutz et al. 1991). A more important food source, mice and voles, was not included at this time because of the logistical difficulty of measuring the relative abundance of mice and voles in so many different localities. I studied the availability of burrows because all owls on the study area appear to nest in burrows (but see Cavanagh 1990). American badger (*Taxidea taxus*) burrows are sufficiently large to be used by the owls directly; ground squirrel (*Spermophilus* sp.) burrows need to be enlarged. I also recorded the extent of cultivation because it is thought to reduce habitat quality for the owls (Wedgewood 1976).

STUDY AREA AND METHODS

The study area was within a large expanse of rangeland used for grazing cattle. Approximately 15% of land was under cultivation for dry-land crop production. This region of mixed-grass prairie experiences low annual rainfall (27 cm) and for this reason sparse and short vegetation predominates. The gently undulating landscape supports a mixed *Stipa-Bouteloua-Agropyron* community with needle and thread grass (*Stipa comata*) and western wheatgrass (*Agropyron smithii*) prevailing (Smoliak et al. 1985). At one site of native grassland where burrowing owls nested regularly since at least 1986, the characteristic brown solonetzic soil had a 15-cm deep A-horizon of sand and a 13-cm deep B-horizon of clay. Especially in the clay layer, the generally dry soil is so well packed that it presumably presents significant barrier to excavation by burrowing owls.

I visited 34 nests at which at least one young was raised; 28 nests between 30 June–18 July in 1989 and six nests between 5–13 July in 1990. For comparison with occupied nests, I selected a "control" site 1 km north, except for seven nests which were in close proximity of one another, yielding 27 control sites. Although these control sites may be considered within an owl's 2.41 km^2 average home range (Haug and Oliphant 1990), home ranges can overlap greatly in this species. If the central point of a control site fell into a cultivated field, I selected a site to the east instead. Because of this choice the data from the control sites may underestimate the extent of cultivation in the region. However, this approach may make the comparisons from the point of view of what kind of habitat is available to burrowing owls more valid. Burrowing owls on the study area sometimes nested near a field, but to my knowledge not within it.

I recorded grasshopper numbers and amount of vegetation within a 30 × 30 cm wire frame (0.09 m^2) tossed onto the ground at 10 m and 70 m from a nest or control site in each of the four cardinal directions. Many insects leapt as the wire frame touched the ground; those that remained were forced to move by stroking a hand over the ground. It proved impossible to identify the insects and count them at the same time. Therefore, I counted all insects that leapt from the ground within the wire frame. These potentially included grasshoppers (Acridoidea), leafhoppers (Cicadellidae) and froghoppers (Cercopidae). Vegetation was described as "barren" if the amount was judged <5 g/plot. When >5 g, live and dead stalks were cut at ground level and weighed on site.

Burrow openings, judged to be those of ground squirrels or badger (width >20 cm) according to size, were counted while driving a motorcycle along two 2 × 500 m line transects, extending north and south away from the burrow or the center of the control site. Within a 0.79-km^2 circle surrounding the nest or control site, I visually estimated the percentage of grassland, shrubland and cultivated land. This was done separately for each quarter circle and then summed.

I used contingency tables in the statistical analysis. I collapsed rows until no more than 20% of expected values were <5 (Conover 1971:152). I rejected the null hypothesis at $P < 0.05$.

RESULTS AND DISCUSSION

This study assumes that the habitat near burrowing owl nests is important to the owls not only for nesting, but also for feeding. While at least one member of an owl pair may range from 0.14–4.81 km^2 (Haug and Oliphant 1990) in search of food, Schmutz et al. (1991) have observed owls at at least 19 nests in the study area hunting insects from a vantage point near the nest.

Leaping insects and adult grasshoppers that flew ranged in length from approximately 2–15 mm. Although the majority of these insects were smaller than 4 mm, it is likely that most were actually grasshopper nymphs which could become large enough later to be used as food by the owls. Numbers of "grasshoppers" on plots varied from 0–15. Numbers were similar at 10 m (4.5/plot) and 70 m (4.9/plot) distances from nests. Using plots at 10 and 70 m distances combined, there was no significant difference between densities around nests compared with control sites (Table 1). These results suggest that grasshoppers were widely available throughout the study area. Therefore, it may be unlikely that grasshopper abundance, at least during the fledgling period, limited owl numbers.

Because avian and mammalian predators prey on burrowing owls, the availability of a suitable burrow for nesting or escape may be an important prerequisite (Coulombe 1971, MacCracken et al. 1985). Since it was impossible to judge the suitability of burrows for use by owls, I recorded all burrows when at least the entrance was open. I included ground squirrel burrows because the larger of these could conceivably be used by the owls. The abundance of ground squirrel burrows may also reflect badger activity and ground suitability for digging.

Burrows of ground squirrels and American badg-

Table 1. Density of grasshoppers, number of burrows and percent cultivation in the vicinity of 34 nests used by burrowing owls and 27 systematically selected sites in southeastern Alberta, 1989–90.

Variable	Nest			Control Site					
	Mean	SD	Range	Mean	SD	Range	χ^2	df	*P*
Grasshoppers	4.7	2.9	0–15	5.1	3.0	0–12	3.37	4	0.498
Burrows									
Squirrel	43.4	19.5	12–75	35.2	16.9	4–70	2.43	2	0.297
Badger	5.2	3.7	1–16	4.7	4.0	0–17	0.80	3	0.850
Grassland (%)	78.9	19.2	38–100	85.0	14.8	38–100			
Shrub cover (%)	4.8	3.7	0–13	6.2	4.2	0–15			
Cultivation (%)	16.3	19.0	0–60	8.8	15.6	0–62	2.23	2	0.328

er were abundant throughout the grasslands on the study area. A minimum of four ground squirrel burrows were present on all nest and control transects (Table 1). Only 4 of the 27 control transects had no badger burrow. While burrows of both badger and ground squirrels tended to be more numerous near nests in comparison to control sites, these differences were not statistically significant (Table 1). Thus, it is unlikely that burrow availability limited the breeding density of the owls.

Loss of habitat through land cultivation is thought to influence the distribution of burrowing owls (Wedgwood 1976). In contrast, Haug and Oliphant (1990) found that while fields with standing crops were avoided, so were overgrazed pastures. Fallow fields were used in proportion to availability. Cultivation on the study area resulted in large, widely scattered fields, either with crops growing or fallow. Patches of shrubs (primarily snowberry, *Symphoricarpos albus*) were generally small but frequent (present in 95% of nest and control areas combined). Of the nests sampled, 41% were located within 0.5 km of a field compared to 59% of control sites. Although slightly more area was under cultivation near nests (16.3%) compared to control sites (8.8%), there was no statistically significant difference among the percentage categories comparing nest and control sites (Table 1).

To measure a patch's potential ability to sustain the owls' cricetid or insect prey, I recorded the amount of above-ground vegetation present. I assumed that areas with above average amounts of vegetation would provide more escape cover and food for species in the owls' food chain (e.g., voles; Bock et al. 1984). Although fewer of the control sites (61.5%) compared to nest sites (76.5%; Table 2) were judged barren, this difference was not significant (x^2 = 5.26, df = 2, P = 0.072). These results suggest that systematically selected sites are at least as productive as occupied nesting areas.

The trend for lower vegetation density in the vicinity of nests compared to systematically selected sites may reflect the choices made by burrowing mammals more than burrowing owls. Although the land is largely flat, burrows tended to be more common on the higher and well-drained sites where moisture limitation is most severe. MacCracken et al. (1985) also interpreted differences between vegetation at burrowing owl nests and other sites in relation to burrowing mammals. In their study, the owls chose recently-vacated black-tailed

Table 2. The amount of vegetation in four subsamples each, at distances of 10 and 70 m from 34 burrowing owl nests and 27 control sites in southeastern Alberta, 1989–90.

Category	Nests				Control Sites			
	10 m	70 m	Total		10 m	70 m	Total	
"Barren"	30	22	52	76.5%	17	15	32	61.5%
6–17 g/plot	2	8	10	14.7%	5	5	10	19.2%
18–112 g/plot	2	4	6	8.8%	5	7	12	17.7%
Total	34	34	68		27	27	54	

prairie dog (*Cynomys ludovicianus*) burrows, whose mounds were in early stages of succession.

The habitat parameters studied provide only a narrow window into a variety of potential breeding requirements for burrowing owls. For instance, the parameters did not address the abundance of voles and mice, the influence of predators on site selection, or the change in food abundance throughout the season. This study suggests that if burrowing owl numbers in the region are low because of habitat, the factors causing this limitation are subtle. Future studies into the dynamics of burrowing owl populations should also take a view toward migration and wintering areas in the hope of discovering limiting factors.

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BURROWING OWL DEMOGRAPHY AND HABITAT USE AT TWO URBAN SITES IN SANTA CLARA COUNTY, CALIFORNIA

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ABSTRACT.—Data on several demographic and habitat choice parameters are reported for urban burrowing owls (*Speotyto cunicularia*) living at two sites in Santa Clara County: an "unintentional" preserve at Moffett Federal Airfield and a planned preserve at Shoreline Park. Differences in management practices and land use might be expected to result in significant differences between the owl populations at the two sites. Shoreline owls chose nest burrows in tallgrass fields more often than did Moffett Field birds, while the use of the other habitat types did not differ. The nest burrows themselves showed differences in several features. Owls at Moffett Field nested in burrows under cement or other hard surfaces significantly more often than birds at Shoreline. Shoreline owls were located on a hill or incline significantly more often than those at Moffett Field. Differences in management practices and availability of habitat features may help explain these findings. With respect to adult density, number of young fledged or pairs with emergent young, the very developed Moffett Field site was not found to have lower values than Shoreline Park. These findings indicate that the owls at both sites may be part of the same population. The data also show that urban sites can act as unintentional preserves and support owl populations if habitat features necessary for owls are provided.

KEY WORDS: *burrowing owl*; Speotyto cunicularia; *demography*; *habitat choice*; *urban preserves*.

Demografia y uso del habitat del tecolotito enano en dos sitios urbanos en el condado de Santa Clara, California.

RESUMEN.—Inforamacion sobre parametros demograficos y seleccion del habitat se reportan para el tecolotito enano (*Speotyto cunicularia*) que habitan dos sitios del condado de Santa Clara: una reserva "no intencional" en Moffet Federal Airfield y una reserva planeada en Shoreline Park. Se podria esperar que diferencias en practicas de manejo y uso del suelo resultara en diferencias significantes entre las poblaciones de tecolotes en los dos sitios. Los tecolotes de Shoreline usaron madrigueras en campos de pastizal alto con mas frecuencia que las aves de Moffet Field, mientras el uso de otros habitats diferio. Las madrigueras mostraron diferencias en varios aspectos. Los tecolotes de Moffet Field anidaron en madrigueras bajo cemento u otras superficies duras significativamente con mayor frecuencia que las aves de Shoreline. Los tecolotes en Shoreline se localizaban en cerros o laderas significativamente con mayor frecuencia que los de Moffet Field. Las diferencias en paracticas de manejo y disponibilidad de aspectos del habitat pueden explicar estos resultados. Con respecto a la densidad de adultos, numero de juveniles volantones, o parejas con juveniles emergentes el muy desarrollado Moffet Field no mostro valores mas bajos que Shoreline Park. Estos descubrimientos indican que los tecolotes de ambos sitios son parte de la misma poblacion. Los datos indican que los sitios urbanos pueden actuar come reservas no intencionales y soportar poblaciones de tecolotes si los aspectos del habitat necesarios para los tecolotes son provistos.

[Traducción de Filepe Chavez-Ramirez]

The western burrowing owl (*Speotyto cunicularia hypugaea*) is a small bird of prairie habitats which lives east of the Mississippi, north into Canada and south into Mexico. It is the only owl that routinely nests underground. The western subspecies does not dig its own burrows, but takes over burrows abandoned by colonial rodents such as prairie dogs (*Cynomys* spp.) and ground squirrels (*Spermophilus* spp.) (Zarn 1974), or solitary mammals such as badgers (*Taxidea taxus*) (Green 1983, Haug and Oliphant 1990).

Researchers and wildlife authorities have recognized that western burrowing owl populations are declining (Zarn 1974, Evans 1982, DeSante et al. 1992). Such declines seem to be particularly severe in California (James and Ethier 1989, DeSante et al. 1992), where the owl has Special Concern status.

Although human population growth and activity can affect their populations negatively, burrowing owls are quite tolerant of human presence and can adapt to human-altered landscapes (Wesemann and Rowe 1987; Trulio 1992). Burrowing owls are well-known inhabitants of airports, golf courses, school yards, and other short-grass habitats which provide burrows and a prey base (Thomsen 1971, Coulombe 1971, Trulio 1992). The fact that the Florida subspecies (*S. c. floridana*) has been increasing in some parts of urbanized Florida (Wesemann and Rowe 1987, James and Ethier 1989, Millsap pers. comm.), shows that healthy owl numbers and a large human population are not incompatible, at least up to a point (see Wesemann and Rowe 1987).

Despite their presence in urban habitats, it is not known whether western owl populations can persist in severely human-altered environments or what conditions may support their long-term survival. Studies of western burrowing owls in natural environments have provided data on demographics (Thomsen 1971, Coulombe 1971), habitat characteristics (see Zarn 1974 for review) and factors influencing burrow choice (Green 1983, Rich 1986). However, there has been little research on the factors leading to persistence or extinction of western burrowing owls in urban environments.

This paper presents data from a 3-year study of urban burrowing owls and compares two sites in Santa Clara County, California. The first, Moffett Federal Airfield, is an "unintentional" owl preserve with numerous military base activities including those related to the Navy airfield and NASA aircraft testing. The second site is Shoreline Park, a planned preserve and recreation area adjacent to Moffett Field, which supports activities such as golfing, hiking and biking. Much of the park is managed for wildlife use.

Given the different uses and management, the two sites might be expected to differ in demographic parameters and habitat choice by burrowing owls. As a park and wildlife preserve, Shoreline might be expected to provide higher quality habitat than Moffett Field and, therefore, support more owls per acre with a higher reproductive output. Owls at both sites should prefer undisturbed shortgrass fields and avoid tallgrass areas without perches. However, owls at Moffett Field might use tallgrass areas more often than Shoreline birds in order to escape human disturbances. Owls at Moffett Field might also choose burrows with features, such as a cement surface or a nearby fence, which could provide protection from surface disturbances. Possible differences between the two sites were tested with the following null hypotheses: Ho (1): Use of habitat types by nesting owls does not differ significantly between the two sites; Ho (2): Two features of nest burrows, location under a hard surface or on an elevation, do not differ significantly between the two sites; Ho (3): The reproductive output per pair at Shoreline is not significantly higher than Moffett Field; and Ho (4): The density of adult birds at Shoreline is not significantly higher than Moffett Field.

STUDY AREAS

Moffett Federal Airfield and Shoreline Park are located in Santa Clara County, 72 km south of San Francisco. Moffett Field is approximately 683 ha in size, of which approximately 250 ha are owl habitat. This base supports a large airfield with three aircraft hangers, NASA facilities, numerous administrative and residential buildings and is a Superfund site in the process of site identification and remediation. The primary human disturbances to owls include aircraft activity, grassland management practices such as discing, building and road construction, and daily human activity. Before 1 July 1994, approximately 8000 people worked at the base each day. California ground squirrels (*Spermophilus beecheyi*) are occasionally controlled in residential, administrative, and golf course areas using traps, but not regularly in areas that are without turf—a policy that has resulted in a large population of ground squirrels at the base.

Shoreline Park is a regional recreation and wildlife area established on a landfill which officially closed in 1983. The park is directly west of Moffett Field, and is separated from the base by an estuarine slough. Shoreline Park contains approximately 112 ha of potential owl habitat, including 38 ha of tall grassland and a 24 ha golf course. Much of the open grassland is managed for wildlife, particularly burrowing owls, by protecting undisturbed plant communities, prohibiting habitat destruction and restricting pedestrians. No poisons are used to kill squirrels and they are left undisturbed, except on the golf course where mechanical traps are used. Poisons are used occasionally to kill pocket gophers. The park receives up to a million visitors per year, or an average of 3000 people/day.

METHODS

Results cover the period from 1 January 1992–15 September 1994. Surveys of nearly all open lands at both sites were conducted on foot between

January and March of each year to locate occupied owl burrows. Burrows were recognized by the presence of owls or owl sign such as pellets and white droppings. All burrows and possible perching posts encountered were examined. Until approximately 15 September each year, at least half the known owl burrows were checked weekly for the number of adults and chicks. Two nesting burrows were observed each week for at least 2 h during the morning (700–1100 h) or evening (1600–2100 h) to get an accurate chick count and record behavior. Observations were made from cars or on foot using 10 × 50 binoculars. Burrow features recorded for this study included distance of burrows above grade and the presence of hard surfaces or fences. Chicks were considered fledged when they could fly strongly, which usually occurred 3–4 wk post-emergence.

Of the approximately 250 ha of owl habitat at Moffett Field, approximately 152 were included in the study. Approximately 112 ha of owl habitat at Shoreline were routinely surveyed.

Open, unpaved sites with burrows were considered potential owl habitat. Habitat was divided into four categories based on general vegetation management practices employed during the nesting period: short-grass (mowed or groundcover), tall-grass (unmowed), disced land, and barren (sprayed or graded).

At Moffett, tallgrass vegetation was never mowed or mowed only once during the nesting season and consisted primarily of Russian thistle (*Salsola kali*), star thistle (*Centaurea solstitialis*) and nonnative annual grasses which grew to a height of approximately 60–90 cm. The primary tall grass in the park, perennial rye grass (*Lolium perenne*), grew to a height of approximately 60 cm and was never mowed. In July 1992, NASA disced most of its open fields; i.e. plowed the top 10–15 cm of soil. Barren lands were levees, berms, road edges or fields which were often sprayed to remain vegetation-free. The total area of berms, road edges and bare earth could not be accurately determined at either site. Levees, a subset of barren lands, could be measured and this habitat type was used to indicate the extent to which owls nested in barren areas. Levees are embankments with water at the base during some period of the year.

z-scores were used to determine whether habitats were used in accordance with their availability and whether burrow features at Shoreline differed significantly from those at Moffett Field ($P = 0.05$).

Table 1. Relative use of habitat types by adult owls at Shoreline Park and Moffett Field, 1992–94.

Habitat Type	% Total Area	% of Nest Burrows	Significance[a]
Shoreline			
Short grass	43%	29%	$z = -1.55$, NS
Tall grass	39%	32%	$z = -0.77$, NS
Levee[b]	11%	29%	$z = -3.00$, S
Disced	3%	7%	$z = -1.33$, NS
Moffett			
Short grass	28%	33%	$z = -1.00$, NS
Tall grass	65%	15%	$z = -8.33$, S
Levee[c]	4%	16%	$z = 5.00$, S
Disced[d]	18%	9%	$z = -0.88$, NS

[a] NS = not significant; S = significant.
[b] Amount of barren area could not be estimated, but contained 10 nest burrows. Levee habitat is used as an indicator of owl use of barren habitat.
[c] Amount of barren area could not be estimated, but contained 35 nest burrows. Levee habitat is used as an indicator of owl use of barren habitat.
[d] Disced lands occurred in 1992 only; percentages calculated for 1992 burrows and habitat.

T-tests were used to assess the difference between fledging success at the two sites.

Results

Table 1 provides the percentage of each potential owl habitat type at the two study sites and owl use of each habitat as measured by the presence of a nest burrow. Levee habitat was used as an indicator for owl use of barren sites. At Moffett Field, owls used levee habitats significantly more than expected based on their availability and significantly underused tallgrass sites. Mowed and disced sites were used in proportion to their availability. Shoreline owls used levee areas significantly more than expected and all other habitats in proportion with their availability.

Nest burrows at Moffett Field and Shoreline showed significant differences. At Shoreline, 68% of nests (21 of 31) were located on an incline or a mound, compared to 41% (28 of 69) Moffett Field nests, a significant difference ($z = 3.85$, $P = 0.05$). Nest burrows ($N = 9$) in hills or mounds in tallgrass habitat at Shoreline were an average of 1.4 m in elevation above the base of the hill. At Moffett Field, 45% or 31 of 69 burrows were located under a hard surface such as asphalt or behind a fence.

Table 2. Abundance and reproductive success of burrowing owls at Shoreline Park, 1992–94.

	1992	1993	1994[a]
Number of adults total[b]	23	20	13
Number of pairs total[b]	11	9	5
Pairs regularly observed	9	8	4
Pairs with emergent chicks	7	7	3
Percent of pairs with emergent chicks	78	88	75
Number of chicks fledged	21	15	14
Average number fledged/brood	3.0	2.5	4.7
Density of adults/ha	0.12	0.18	0.15

[a] Golf course excluded in 1994 from survey (24 ha).
[b] Only birds seen on more than one occasion were counted.

At Shoreline, only 19% of nest burrows (6 of 31) were similarly protected, significantly fewer than at Moffett Field (z = 4.33, P = 0.05).

Abundance and reproductive data for Shoreline and Moffett Field are given in Tables 2 and 3, respectively. Data from the two sites were comparable. Over the three years, Shoreline supported an average of 21 adults on approximately 112 ha, for an average density of 0.19 owls/ha. Of pairs observed, an average of 79% had emergent chicks. Over the three years, an average of 2.9 chicks were fledged/brood. Moffett Field supported an average of 43 adults on 152 ha for an average density of 0.28 adult owls/ha during the 3-year study period. The 3-year average for percent of pairs with emergent chicks was 75%, and the average number of chicks fledged was 2.5 chicks/brood. The average number of chicks fledged did not differ significantly between Shoreline and Moffett Field (t = 0.975, df = 15, P = 0.05).

DISCUSSION

Burrowing owls prefer open habitats or locations with perches which afford a good view of approaching predators (Zarn 1974, Green 1983). Green (1983) found that owls in Oregon avoided habitat with vegetation that impaired the owls' horizontal visibility and did not provide suitable perches. Habitat choice by owls at Moffett Field and Shoreline reflected these observed preferences, as owls at both sites used short grass habitat in proportion to its availability and nested on levee sites significantly more than expected. However, owls significantly underused tallgrass sites at Moffett Field, while Shoreline owls used tallgrass habitat in proportion with its availability. This difference resulted in the rejection of Ho (1), but not for the reasons expected. Owls at Moffett did not escape to tallgrass sites to avoid human impact, perhaps because they could not find burrows above the vegetation. Shoreline owls, on the other hand, were able to exploit tallgrass habitat by occupying burrows on mounds or an elevated site. Every burrow in tallgrass habitat at Shoreline was elevated above grade (10 of 10 burrows), while only 20% (2/10) of burrows in Moffett Field's tallgrass habitat were elevated.

Table 3. Abundance and reproductive success of burrowing owls at Moffett Field, 1992–94.

	1992	1993	1994
Number of adults total[a]	39	49	42
Number of pairs total[a]	19	23	19
Pairs regularly observed	15	19	19
Pairs with emergent chicks	11	14	15
Percent of pairs with emergent chicks	73	74	78
Number of chicks fledged	27	34	38[b]
Average number fledged/brood	2.5	2.4	2.9[b]
Density of adults/ha	0.26	0.32	0.26

[a] Only birds seen on more than one occasion were counted.
[b] Full counts of fledged chicks made on 13 pairs, which fledged 38 chicks total.

In general, the use of burrows on mounds or elevated sites differed between the two sites. Although mound availability could not be quantified at either site, it is likely that mounds and hills are less prevalent at Moffett Field than Shoreline. In the past, much of Moffett Field was leased as farmland and plowing fields would have flattened any mounds. As a closed landfill, Shoreline has never been farmed and when it was closed, the surface was purposely contoured to provide hills.

The use of tallgrass habitat at Shoreline and preferential use of levees at both sites suggest that the presence of mounds or elevation can increase the owl occupancy of a habitat. Levees are particularly attractive nest sites, since in addition to elevation, they are usually vegetation-free, well populated by ground squirrels and protected from flooding.

Disced lands were used in accordance with availability at both sites, but the small amount of area disced may not have allowed adequate statistical analysis.

Use of elevated burrows by Shoreline owls was one burrow feature which differed significantly between the two sites, resulting in the rejection of Ho (2). Another significant difference was the proportionately greater use of burrows under hard surfaces by Moffett Field birds versus Shoreline owls. It is likely that such burrows are more common at the very developed Moffett Field site, but this factor remains to be quantified. It is also possible that owls located under hard surfaces at the base may be more likely to survive disturbances than those not so protected. For example, discing fields can disturb or destroy owls nesting there (J. Buchanan pers. comm., J. Priest pers. comm.) and until 1993 many fields at the base were disced. Most of Shoreline has never been disced, sparing owls this pressure. Two fields outside the park included in the study are always disced and each year owls in those fields were located under a cement surface at the edge of the field. In natural habitats, owls use burrows under rocks (Rich 1984), lava flows (Gleason and Johnson 1985) and limestone (Coulombe 1971), perhaps as a protection against digging predators (Rich 1984).

Although habitat use and burrow features differed between the two sites, this study did not reveal differences in demographic parameters. Reproductive output values at the preserve were not significantly higher than at the more developed site. Although adult density at the two sites could not be statistically compared, Moffett Field actually had a denser population than Shoreline. Neither Ho (3) nor Ho (4) could be rejected, suggesting that both sites currently offer suitable habitat for owl survival and reproduction. This finding is very intriguing since the sites seem to differ so much in activity level.

While activities may differ, there are some important similarities. The general level of human and auto traffic at Moffett Field seems similar to Shoreline. In potential owl habitat, Moffett has approximately 0.07 km of roads/ha, compared to 0.06 km of roads and paved pathway/ha at Shoreline. An average of 3000 people visit Shoreline daily (16.5 people/ha) compared to the approximately 8000 people employed people at Moffett (21.9 people/ha) (Dept. of Navy, 1990). People and active land uses at both sites are restricted to specific areas, while the large, open areas where owls tend to live are generally less disturbed.

Other aspects of land management at Moffett Field help provide habitat of similar quality to Shoreline. Large areas of tallgrass provide foraging habitat; other areas are constantly kept short and provide nesting habitat; and ground squirrels are abundant on the open fields and golf courses.

The similar demographic results may also indicate that Shoreline and Moffett owls are part of the same population. The two sites are immediately adjacent to each other with no barriers to owl movement between them and owls may be sharing the positive and negative features of both areas. On a larger scale, the abundance and reproductive success of owls at the two sites may be reflecting conditions of the greater Santa Clara Valley region.

This study suggests that owls can survive on very urbanized sites, which can function as unintentional reserves, if those sites are managed to provide features required by owls. Such features include large open fields for foraging and short-grass sites for nesting. These data suggest that habitat can be enhanced for owls by installing dirt mounds and allowing ground squirrels to dig burrows. Artificial burrows in mounds can be used to provide immediate nest sites for owls (Henny and Blus 1981, Trulio 1992). Burrows under hard surfaces may attract nesting birds and protect them from inadvertent disturbances. Mowing around nest burrows and restricting constant foot or auto traffic help keep sites attractive to nesting owls. Avoiding biocide use is important for ensuring healthy populations of other species upon which owls depend.

Ultimately, integrating burrowing owl habitat into urban environments may prove to be an important method for protecting this species.

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BURROWING OWL SEXUAL AND TEMPORAL BEHAVIOR DIFFERENCES (ABSTRACT ONLY)[1]

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ABSTRACT.—In the field season of 1992, a night-vision scope was used to collect burrowing owl (*Speotyto cunicularia*) behavioral data during darkness comparable to that collected in daylight. Diurnal and crepuscular/nocturnal behaviors, particularly foraging behaviors, were split into prehatch and posthatch seasons and analyzed separately. During the prehatch period, preliminary investigations showed that prehatch comfort movements (e.g., preening, stretching) ($P = 0.0054$), resting ($P = 0.0097$), and alert ($P = 0.0059$) behaviors were greater diurnally, while out-of-sight ($P = 0.0021$) and feeding ($P = 0.0035$) were greater during crepuscular/nocturnal hours. During the posthatch period burrowing owls locomoted more nocturnally ($P = 0.0002$) and performed comfort movements more frequently diurnally ($P = 0.0042$). When the sexes were analyzed separately, females rested ($P = 0.0127$) more during daylight in the posthatch period. Foraging bouts when an owl returned with a small mammal ($\bar{x} = 327$ seconds) were longer ($P = 0.0001$) than those resulting in an insect capture ($\bar{x} = 205$ seconds). Male foraging bouts ($\bar{x} = 257$ seconds) were also longer ($P = 0.0001$) than female ($\bar{x} = 193$ seconds). Males took more small mammals proportionally (15%) than did females (2%) ($P < 0.05$). Results indicate increased burrowing owl foraging activity of both small mammals and insects at dusk and into nightfall.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *behavior; foraging.*

Diferencias de conducta por sexo y temporales de Tecolotito Enano

RESUMEN.—Un telescopio de vision nocturna se utilizo para colectar informacion de la conducta del tecolotitio enano (*Speotyto cunicularia*) durante periodos de obscuridad para comparar con datos collectados durante el dia. Conducta diurna y crepuscular/nocturna, particularmente conducta de forageo, se dividieron en temporadas antes y despues del empollo y se analizaron por separado. Durante el periodo antes de la salida del huevo, investigaciones preliminares mostraron que moviminetos de comodidad (estirar, arreglo de plumas) ($P = 0.0054$, descanso ($P = 0.0097$) y alerta ($P = 0.0059$) eran conductas mas comunes durante el dia, mientras que las categorias fuera de vista ($P = 0.0021$) y comer fueron mayores durante horas crepusculares/nocturnas. Durante el periodo despues de la salida del huevo los tecolotitos mostraron mas locomocion durante la noche ($P = 0.0002$) y realizaron movimientos de comodidad con mas frecuencia durante el dia ($P = 0.0042$). Cuando los sexos se analizaron por separado, las hembras descansaron ($P = 0.0127$) mas durante el dia durante el periodo despues de la salida del huevo. Tiempos de forageo cuando el tecolote retorno con un pequeño mamifero ($\bar{x} = 327$ segundos) fuerom mas largos ($P = 0.0001$) que aqeullos que resultaron en la captura de un insecto ($\bar{x} = 205$ segundos). Los machos capturaron mas pequeños mamiferos proporcionalmente (15%) que las hembras (2%) ($P < 0.05$). Los resultados indican que la actividad de forageo del tecolotito enano de insectos y mamiferos aumenta durante la puesta del sol y en la noche.

[Traducción de Filepe Chavez-Ramirez]

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[1] For further details see Pezzolesi, L.S.W. 1994. The western burrowing owl: increasing prairie dog abundance, foraging theory, and nest site fidelity. Master's thesis. Texas Tech. Univ., Lubbock, TX.
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TERRITORY FIDELITY, MATE FIDELITY, AND DISPERSAL IN AN URBAN-NESTING POPULATION OF FLORIDA BURROWING OWLS

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ABSTRACT.—From 1987–91 we studied an urban population of Florida burrowing owls (*Speotyto cunicularia floridana*) on a 35.9-km^2 study area in Cape Coral, Lee County, Florida. During this period our study population increased from 149 occupied territories in 1987 to 246 in 1990; a total of 785 nesting attempts was monitored. From 1987–90, 601 owls, about 25% of breeding adults and 20% of nestlings in each year, were banded. Nearly all banded breeding adults were identified in subsequent years, and 245 individuals were reencountered at least once. Reencounter rates averaged over the years 1988–91 were 68% for adult males, 59% for adult females, and 19% for owls banded as nestlings. Natal dispersal distances differed significantly between sexes. The median natal dispersal distance was 414 m for males and 1116 m for females. About 36% of males settled on their natal territories, and at least 11% mated with their mothers; only one female (3%) settled on her natal territory. Adults had a high degree of fidelity to breeding territories, with 83% of males and 74% of females breeding on the same territories for at least two consecutive years. Territory fidelity appeared to increase with age in both sexes. There were no clear patterns that preceded territory shifts, except that females usually moved to a new territory after the death of a mate, whereas males generally stayed on the same territory regardless of the status of their prior mate. When breeding dispersal did occur, females moved further than males; median breeding dispersal distance was 230 m for females and 96 m for males. Among pairs where both adults survived between years, 92% remained together. Patterns of dispersal and territory and mate fidelity in our study population suggest male experience on a given territory may be an important factor in determining reproductive success.

KEY WORDS: *burrowing owl;* Speotyto cunicularia floridana; *fidelity; nesting; Florida; dispersal; urban.*

Fidelidad territorial, fidelidad de pareja, y dispersion en una poblacion de tecolotitos enanos de Florida en un area urbana

RESUMEN.—De 1987 a 1991 estudiamos una poblacion urbana de tecolotito enano (*Speotyto cunicularia floridana*) en una area de estudio que comprendia 35.9-km^2 en Cape Coral condado de Lee, Florida. Durante este periodo nuestra poblacion de estudio aumento de 149 territorios ocupados en 1987 a 246 en 1990; un total de 785 atentos de anidacion se monitorearon. De 1987 a 1990, 601 tecolotes, aproximadamente 25% de los adultos reproductores y 20% de los pollos en cada año se anillaron. Casi todos los adultos anillados fueron identificados en años subsequentes y 245 individuos se encontraron cuando menos una vez. La tasa promedio de reencuentro para los años 1988–91 fueron de 68% para machos adultos, 59% para hembras adultas, y 19% para tecolotes anillados en el nido. Distancias de dispersion natal diferieron significativamente entre los sexos. La distancia media de dispersion natal fue de 414 m para machos y 1116 m para hembras. 36% de los machos se establecieron en sus territorios natales y al menos 11% aparearon con sus madres; solo una hembra (3%) se establecio en su territorio natal. Adultos tuvieron alta fidelidad a sus territorios de reproduccion con 83% de machos y 74% de las hembras reproduciendose en el mismo territorio cuendo menos 2 años consecutivos. Fidelidad a territorios parece ser mayor con edad en ambos sexos. No hubo patrones claros que anticipara cambios en territorios, excepto que hembras usualmente se cambiaron a un nuevo territorio despues de la muerte de su pareja mientras los machos generalmente permanecian en el mismo territorio, sin importar la condicion de su previa pareja. Cuando dipsersion reproductiva ocurrio, las hembras se desplazaron mas lejos que los machos. De las parejas en las que ambos adultos sobrevivieron entre años 92% se mantuvieron juntas. Patrones de dispersion y fidelidad territorial y de pareja en nuestra poblacion sugiere que la experiencia del macho en determinado territorio es un importante factor que determina exito reproductivo.

[Traducción de Filepe Chavez-Ramirez]

Despite its wide range and history of scientific interest, many aspects of the biology of the burrowing owl (*Speotyto cunicularia*) remain poorly understood. This is particularly true for nonmigratory subtropical and tropical populations of this widespread species. Although the burrowing owl is garnering conservation attention throughout much of its North American range, it is significant that at least two Caribbean island populations of this species have gone extinct in recent times (AOU 1957).

The Florida burrowing owl (*S. c. floridana*) is an extant subtropical population that is of some concern. This race of burrowing owl occurs throughout peninsular Florida and the Bahama Islands. Unlike most western burrowing owl populations, Florida burrowing owls usually excavate their own nest burrows, although they will use burrows of gopher tortoises (*Gopherus polyphemus*) and nine-banded armadillos (*Dasypus novemcinctus*) when available (Haug et al. 1993). As with many other arid-adapted taxa in Florida, burrowing owls probably colonized the state from western North America during early- to mid-Pleistocene glacial periods when a circum-Gulf arid dispersal corridor existed (Webb 1990). Florida burrowing owl populations have probably been isolated since the close of the Wisconsinan stage of the Pleistocene, which was at its height 20 000 years before the present (Webb 1990). Early records of burrowing owls in Florida were mainly from the central peninsula (Ridgway 1914, Bent 1938). Burrowing owls began a range expansion in Florida in the 1940s that continues to the present, presumably facilitated by land-clearing operations along the coasts and in the northern peninsula and panhandle. In the early 1940s burrowing owls were found breeding in Hernando County in west-central Florida (MacKenzie 1944), by 1954 nesting was documented in Marion County in northcentral Florida (Neill 1954), and in 1992 a breeding population was discovered in the Florida panhandle in Okaloosa County (B. Millsap unpubl. data).

Despite its expanding range, the Florida Game and Fresh Water Fish Commission lists the Florida burrowing owl as a Species of Special Concern (Wood 1992), and the agency has initiated several conservation projects for this subspecies. One of the greatest perceived threats to this race is habitat development and resultant land use changes. Ironically, the very land use changes that create suitable new habitat for burrowing owls in Florida also destroy it, and there are many cases where thriving local populations have become extirpated over the span of a few years (Courser 1976). To better understand the causes of burrowing owl population changes in developing areas, the Game and Fresh Water Fish Commission and Audubon Society of Southwest Florida initiated a study of burrowing owls in an urbanizing area of southwest Florida in 1987. Wesemann and Rowe (1986) conducted preliminary work on this study population in 1985 and 1986; we continued and expanded their work to include banding and monitoring adults and young and determining reproductive success. This paper presents information collected on dispersal and mate and territory fidelity in this study population.

STUDY AREA AND METHODS

Observations were made between 1 January 1987 and 10 July 1991 on a 35.9-km^2 study area in Cape Coral, Lee County, Florida (Fig. 1). The study area consisted mainly of single-family homes interspersed with vacant lots. Vacant lots, where most nest burrows were situated, were maintained as disclimax grasslands by regular mowing. Climate in Cape Coral is subtropical, with an annual mean temperature of 23.1°C. Temperatures below 0°C are rare; lowest daily mean temperature for January (the coldest month) is 10.9°C. Precipitation averages 125.7 cm annually, and 75% of rainfall occurs between May–September (climate data from NOAA climatological data summaries for Fort Myers, Florida, 20 km southeast of the study area).

From January–March, 1987–91, we drove all roads in the study area searching for burrowing owl nest burrows. This approach is known to locate all but a small percentage of nests (Wesemann and Rowe 1987). Burrows attended by two adult owls or decorated with shredded paper and grass were considered occupied territories. Data on the number of occupied territories on our study area in 1986 were collected using methods described by Wesemann and Rowe (1987). From 1987–90, adult and juvenile burrowing owls were captured with noose carpets placed at the burrow entrance and banded with U.S. Fish and Wildlife Service bands and colored leg bands. Nearly all adults attending nests on the study area were checked for bands annually from 1988-91. Additionally, from 1988–90, we searched for banded burrowing owls at territories in a 3.2-km-wide band immediately north of our study area, as well as south of our study area to the

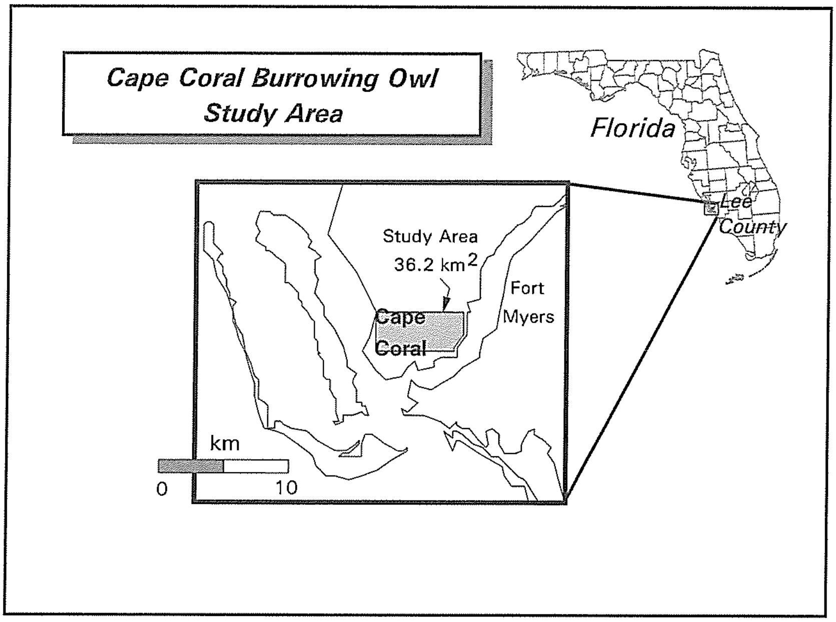

Figure 1. Study area in Cape Coral, Lee County, Florida.

southern terminus of the Cape Coral peninsula. When banded owls were resighted on the study area or elsewhere, we confirmed identification by reading band numbers with spotting scopes or binoculars or by retrapping. The sex of breeding adults could usually be determined at a distance by plumage (males were paler than females due to increased sun-bleaching (Thomsen 1971, Butts 1973, Martin 1973)) or behavior (Thomsen 1971). Breeding females with eggs or small young could be distinguished in the hand by the presence of a large, vascularized incubation patch. We were unable to determine the sex of nestlings when they were initially banded, but most that were subsequently reencountered as breeders were sexed. Nests on the study area were visited weekly in the early morning or late afternoon (when owls were active aboveground) throughout the nesting period (mid-February through early July) to determine fledging success and estimate brood size at fledging.

We analyzed data using statistical procedures in SYSTAT (Wilkinson 1990). Parametric procedures were used when raw variates or transformed variates appeared normally distributed. In cases where normality was suspect, we used nonparametric tests. In these cases we report medians as our measure of central tendency and interquartile ranges (i.e., the interval around the median that contains 50% of all observations) as our measure of data dispersion.

We define *natal dispersal* as dispersal by a burrowing owl from the territory where it hatched to the territory where it first bred. *Breeding dispersal* refers to dispersal from a previous breeding territory to a new territory or to a new burrow on the same territory if the prior year's nest burrow was occupied by another pair of breeding adults. The term *reencounter* refers to the identification of an owl banded in a previous year; in numerical tallies, individuals identified in multiple years accounted for multiple reencounters, but no owl accounted for more than one reencounter in any one year. In reporting ages of burrowing owls, we use the following terms: *second year* (SY) for owls in their second calendar year of life; *third year* (TY) for owls in their third calendar year of life; *fourth year* (FY) for owls in their fourth calendar year of life; *after hatching year* (AHY) for owls of uncertain age but at least SY or older; *after second year* (ASY) for owls of uncertain age but at least TY or older; *after third year* (ATY) for owls of uncertain age but at least fourth year (FY) or older; and *after fourth year* (AFY) for owls of uncertain age but in at least their fifth calendar year of life.

RESULTS

Population Size. From 1987–90 we located and monitored 785 occupied burrowing owl territories on our study area. The number of occupied territories increased annually, from 149 in 1987, to 175 in 1988, 213 in 1989, and 248 in 1990. Wesemann and Rowe (1987) reported 133 occupied territories on our study area in 1986. Because our survey efforts and approach remained relatively constant among years, we attribute the increase in the number of occupied territories to an increase in population size over the study period.

Reencounter Rates for Banded Owls. From 1987–90, we banded 601 burrowing owls on our study area: 307 nestlings of unknown sex, 116 adult

Table 1. Reencounter rates for banded Florida burrowing owls, Cape Coral, Florida, 1988–91.

	% Owls Alive Prior Year That Were Reencountered				
Age[a]	1988	1989	1990	1991	Mean (SD)[b]
SY	31	20	17	10	19 (1.2)
>ASY male	79	68	62	64	68 (0.7)
>ASY female	69	61	54	51	59 (0.7)

[a] Age codes are as follows: SY (second year) = burrowing owls banded as unsexed nestlings the prior year; >ASY (after second year) male and >ASY female = burrowing owls of known sex that were SY or AHY the prior year when first banded or when reencountered.

[b] Means were calculated from arcsine-transformed proportions for each year, such that $N = 4$ in each case. Arcsine-transformed mean proportions differed significantly among age/sex categories (one-way ANOVA, $F = 40.4$, df = 2/9, $P < 0.0001$). A Bonferroni post-hoc test indicated that mean reencounter rates for >ASY males and females were not significantly different ($P > 0.05$), but that both differed significantly from the mean reencounter rate for SY owls ($P < 0.0001$).

males, 153 adult females, and 25 adults of unknown sex. Overall, about 25% of breeding adults and 20% of young on our study area were banded each year. From 1988–91 we reencountered 245 (41%) of these owls at least once, 131 (27%) were reencountered in two or more years, 52 (17%) in three or more years, and 11 (8%) in four years. An average of 68% of adult males, 59% of adult females, and 19% of nestlings were known to survive between years (Table 1). Mean reencounter rates differed significantly between established adults and second-year owls, but not between sexes of adults (Table 1).

Natal Dispersal. From 1988–91 we reencountered, as breeders, 31 female and 28 male burrowing owls that had been banded as nestlings. Median natal dispersal distance of females was 1116 m (interquartile range = 440–1725 m); median natal dispersal distance for males was 414 m (interquartile range = 150–850 m) (Fig. 2). Natal dispersal distances differed significantly between sexes (Mann-Whitney $U = 484.0$, df = 1, $P = 0.001$).

The mean distance between nearest adjacent occupied nest burrows on our study area in all years was 176 m (SD = 135.8, $n = 785$). Of the banded nestlings reencountered as breeders, one female

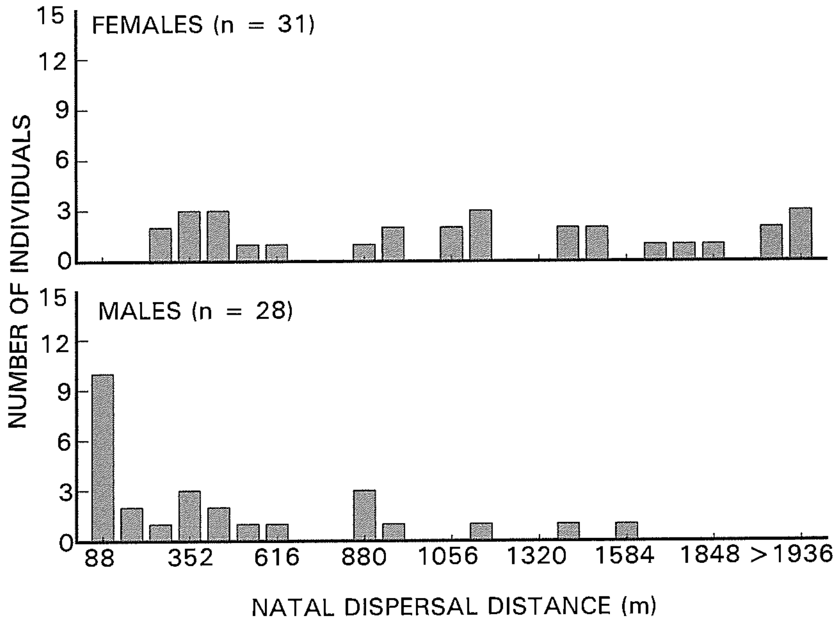

Figure 2. Histogram of natal dispersal distances of burrowing owls from Cape Coral, Lee County, Florida, 1988–91. We defined natal dispersal as dispersal by a burrowing owl from the territory where it hatched to the territory where it first bred.

Table 2. Fidelity to prior year's territory by Florida burrowing owls known to have survived between years, Cape Coral, Florida, 1988–91.

	% OF REENCOUNTERED BIRDS FOUND ON SAME TERRITORY	
AGE[a]	MALE	FEMALE
SY	36 (10/28)	3 (1/31)
ASY/TY	78 (77/98)	68 (69/101)
ATY/FY	91 (42/46)	73 (41/51)
AFY	83 (20/24)	83 (15/18)

[a]Age codes are as follows: SY = second year (individuals in their second calendar year); ASY = after second year (individuals in at least their third calendar year); TY = third year (individuals in their third calendar year); ATY = after third year (individuals in at least their fourth calendar year); FY = fourth year (individuals in their fourth calendar year); AFY = after fourth year (individuals in at least their fifth calendar year).

(3%) and 10 males (36%) nested in their natal burrow or within one-half the mean inter-nest distance (i.e., within 88 m) of their natal burrow. Three of these males (11%) paired with their mother on their natal territory; in only one case was the father banded, and in this instance he was found paired with a new female at a new burrow 20 m away.

Territory Fidelity. From 1988–91, we recorded 399 reencounters of Florida burrowing owls of known sex. Pooled across sex and age classes, 273 (68%) reencountered individuals remained on the same territory between years (Table 2). However, rates of territory fidelity were not independent of age or sex. Among second-year owls, more males than females remained on their natal territory than expected by chance (G = 7.56, df = 1, P = 0.006). For older age classes, territory fidelity was independent of sex (G = 0–2.69, df = 1 for all comparisons, $P > 0.10$ for all comparisons). Age appeared to influence territory fidelity among both sexes. Tested separately, and as would be expected, both male and female SY owls were less prone to remain on their natal territory than older adults were to remain on their prior-year's breeding territory (for males G = 27.9, df = 1, P = 0; for females G = 58.3, df = 1, P = 0). Among adults older than SY, fidelity was not independent of age (G = 6.68, df = 2, P = 0.035). Comparison of simultaneous confidence intervals for proportions using the Bonferroni approach (Byers and Steinhorst 1984) indicated that moves by ASY and TY adults occurred more often than expected relative to moves by adults older than three years of age (sexes were pooled for this analysis because territory fidelity was independent of sex for ASY and older adults).

From 1988–91, 53 reencountered adult males and 57 reencountered adult females vacated a territory, switched burrows on a territory, or moved to a new territory between years. Ten (19%) of the adult males and 12 females (21%) that underwent breeding dispersal were forced to switch territories because their prior year's territory had been destroyed. In most such cases (n = 19, 86%) these sites were destroyed when new homes were built over the prior year's burrow. Among known-sex adults whose prior year's territory was intact, there were no consistent patterns that preceded territory shifts. In fact, more territory moves followed successful breeding attempts (58%, n = 43) than unsuccessful breeding attempts (42%, n = 31; Table 3), although the difference was not statistically sig-

Table 3. Circumstances associated with moves between territories by Florida burrowing owls, Cape Coral, Florida, 1988–91. Does not include moves by 10 males and 12 females after nest territories were destroyed (see text). Values in table are number of reencounters.

	MALE PRIOR YEAR'S SUCCESS		FEMALE PRIOR YEAR'S SUCCESS		
CIRCUMSTANCE	SUCCESSFUL	UNSUCCESSFUL	SUCCESSFUL	UNSUCCESSFUL	TOTAL
Vacated territory and failed to breed	1	0	5	3	9
Moved to new burrow on same territory; prior burrow occupied by other owls	3	0	4	0	7
Mate known to have died	0	4	3	2	9
No known extenuating circumstance	10	11	17	11	49
Total	14	15	29	16	74

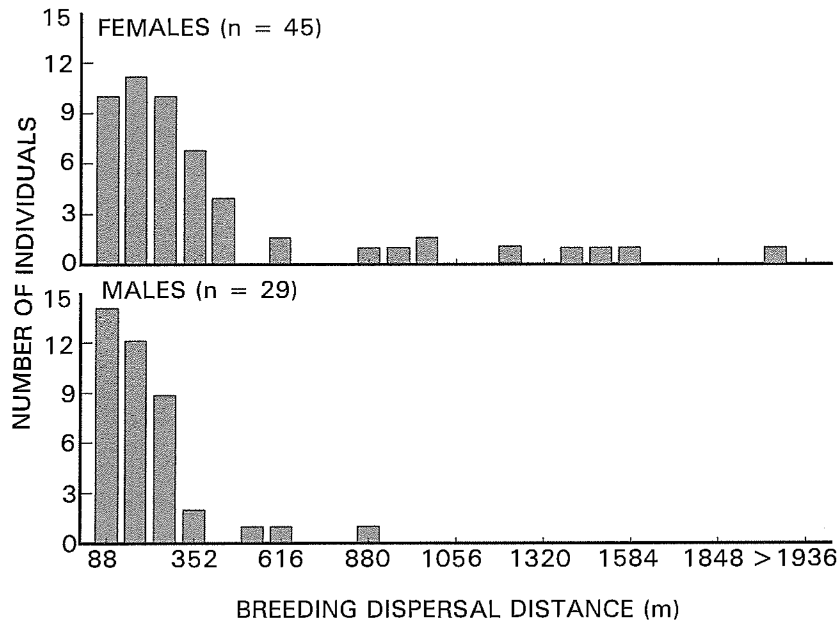

Figure 3. Histogram of breeding dispersal distances of burrowing owls from Cape Coral, Lee County, Florida, 1988–91. We defined breeding dispersal as dispersal from a previous breeding territory to a new territory or to a new burrow on the same territory if the prior year's nest burrow was occupied by another pair of breeding adults.

nificant (χ^2 = 1.94, df = 1, $P > 0.1$). In 57 cases where one adult of a pair where both adults had been banded disappeared (most likely died) and where territories remained viable between years, "widowed" males remained on the same territory the next year 75% of the time (27 of 36 cases), whereas "widowed" females remained on the same territory only 33% (seven of 21 cases) of the time. This indicates that continued residency on a territory after disappearance of a mate was not independent of sex (G = 9.66, df = 1, P = 0.002).

Breeding Dispersal. From 1988–91, 29 reencountered ASY or older male burrowing owls and 45 reencountered ASY or older female burrowing owls shifted territories between years. Median breeding dispersal distance for adult males was 96 m (interquartile range = 71–220 m); median breeding dispersal distance for females was 230 m (interquartile range = 100–413 m) (Fig. 3). Breeding dispersal distance differed significantly between sexes (Mann-Whitney U = 1422, df = 1, P = 0.005).

Mate Fidelity. From 1987–90 we banded both adults of 175 breeding pairs of burrowing owls. At least one adult from 116 (66%) of these pairs was reencountered in a subsequent year. In 57 (49%) of these cases, one member of the pair was not found in any subsequent year. Of the remaining 59 cases where both pair members were known to have survived into the next breeding season, 54 (92%) pairs remained together and 5 (9%) divorced (i.e., separated and paired with other mates). Given rates of territory fidelity in our study population (Table 2), we would have expected only 61% of pairs where both adults survived to have remained together by chance.

DISCUSSION

Natal and breeding dispersal by Florida burrowing owls on our study area was strongly female biased (*sensu* Greenwood 1980). Female natal dispersal distances averaged 2.7 times those of males, and breeding dispersal distances of females averaged 2.4 times as far as for males. This conforms to the general pattern in birds (Greenwood 1980), and is consistent with findings from two Canadian burrowing owl populations (P. James this volume; J. Schmutz unpubl. data).

Among burrowing owls on our study area, territory fidelity was high in both sexes, as was mate fidelity. Some degree of territory fidelity in male burrowing owls has been observed elsewhere (Martin 1973; Haug 1985; P. James this volume). However, in the above-cited studies few burrowing owls retained the same mate between years. In an exception to this trend, Thomsen (1971) reported relatively high mate and territory fidelity among burrowing owls at Oakland, California. Thomsen's (1971) study population, like ours and unlike most others, was nonmigratory. Perhaps high mate fidelity is favored in nonmigratory burrowing owl populations and not in migratory ones.

Our study population had a high rate of male philopatry, with over one-third of all young males settling on their natal territory. In fact, the general pattern appeared to be for a young male to settle on his natal territory if his father died or underwent breeding dispersal. We also observed three cases where fathers excavated new nest burrows on their prior year's territories while their sons bred in their natal burrows 10–50 m away. At least 30% of young males that did not disperse paired with their mothers, and we suspect such matings (which were difficult to detect because only 25% of adults and 20% of young were banded each year) were more common than these data imply.

One major hypothesized function of sex-biased dispersal is avoidance of inbreeding (Greenwood and Harvey 1976, Greenwood 1980). Patterns of burrowing owl dispersal on our study area resulted in no matings between siblings, but many mother-son pairings. Our data show that following the death of a mate, females usually underwent breeding dispersal whereas males did not. Although this could be interpreted as a mechanism to promote avoidance of inbreeding in a population where natal philopatry was common, it might also reflect a premium by females on males with prior experience on a territory. For example, experienced male Eurasian sparrowhawks (*Accipiter nisus*) have been shown to have higher reproductive success than inexperienced males (Newton et al. 1981). However, the same does not always hold true for females. Pietiäinen (1988) determined that female age and experience was not reflected in increased reproductive success in a population of Ural owls (*Strix uralensis*). In our study population, if a resident male burrowing owl died following a reproductive effort producing male offspring, the widow was certain to pair with a male who was unfamiliar with that territory unless she mated with her offspring. If male familiarity with a territory influences reproductive success, it could also explain the potential discrepancy in mate fidelity between migratory and nonmigratory burrowing owl populations. In migratory populations all males may be equally unfamiliar with the current year's distribution of food and cover on their territories upon arriving in spring regardless of their tenure of residency. As a consequence, there may be little advantage in females returning to the same territory to pair with her previous mate. In a future paper we plan to explore the relationship between reproductive success and territory tenure for both male and female burrowing owls on our study area.

ACKNOWLEDGMENTS

These observations were obtained as part of a cooperative burrowing owl monitoring project by the Florida Game and Fresh Water Fish Commission and Audubon Society of Southwest Florida. The work would not have been possible without the dedicated assistance and skill of 23 Audubon Society and Lee County School System volunteers. We also gratefully acknowledge T. Wesemann and M. Rowe for freely sharing the results of their work with burrowing owls in Cape Coral with us, and for encouraging us to undertake this project. This project was funded through the Florida Nongame Wildlife Trust Fund.

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NESTING SITES AND FEEDING HABITS OF THE BURROWING OWL IN THE BIOSPHERE RESERVE OF MAPIMI, MEXICO

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ABSTRACT.—The burrowing owl (*Speotyto cunicularia*) is a threatened species throughout much of its North American distribution, yet little is known about its biology and ecological requirements in Mexico. Nest-site characteristics and feeding habits of this owl were studied over two breeding seasons in the southern Chihuahuan desert, Mexico. A significant correlation was found between nesting success and their location in *Prosopis-Hilaria* grassland "playas," where their prey consisted mainly of invertebrates (such as scorpions, coleoptera, orthoptera) and small mammals (i.e., *Dipodomys, Perognathus, Peromyscus*). Invertebrates were the most frequent prey in the owl's diet (84%), but mammals represented more than 50% of the ingested biomass in both years. The medium prey size was 7.8 ± 4.1 g in 1985 and 5.2 ± 2.5 g in 1986, the differences resulting from a higher predation on reptiles in 1985. Prey diversity was similar in both years ($H'_{1985} = 2.35$; $H'_{1986} = 2.13$), with moderate evenness ($J' = 0.6$) indicating that *S. cunicularia* in Mapimí consumes a relatively diverse array of prey species in relatively even proportions. As in other areas of America, this owl fed mainly on small prey, but some differences were noted interregionally in both the occurrence of prey and ingested biomass. These differences seem to be related to the regional differences in prey abundance and availability. Reptiles were more important in the diet of burrowing owls in Mapimi compared to other regions.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *nesting; feeding; Mapimi Reserve; Mexico; Chichuahuan Desert.*

Sitios de anidamiento y habitos alimenticios del tecolotito enano en la Reserva de la Biosfera de Mapimi, Mexico.

RESUMEN.—La información sobre la biología y requerimientos ecológicos de la lechucita de madrigueras, *Speotyto cunicularia,* es escasa o inexistente en México, aunque es una especie amenazada en la mayor parte de su distribución en Norte América. En este trabajo se presenta información sobre las características de los sitios de anidación y los hábitos alimentarios de la lechucita de madrigueras durante dos épocas reproductivas (1985, 1986) en la parte sur del desierto Chihuahuense en México. Se encontró una correlación significativa entre el éxito reproductivo y la presencia de nidos en la asociación vegetal del pastizal con *Prosopis-Hilaria.* Las presas principales de este búho fueron principalmente invertebrados (alacranes, coleópteros, ortópteros), aunque también pequeños mamíferos (roedores). Los invertebrados representaron el 80% de las presas en su dieta, pero los mamíferos le aportaron más del 50% de la biomasa consumida en ambos años. El tamaño medio de presa fue mayor en 1985 aparentemente debido a una mayor depredación de reptiles. La diversidad de presas fue similar entre años. La lechucita de madrigueras del desierto de Mapimí consume una diversidad de presas superior a la reportada para otras áreas de su distribución, representando los reptiles una mayor importancia en su dieta en relación a las otras regiones. Estas diferencias parecen relacionarse a las diferencias regionales en la abundancia y disponibilidad de presas.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl, *Speotyto cunicularia,* has a widespread distribution in grasslands throughout the Americas (Johnsgard 1988), although it is a threatened species in Canada and in some states of the U.S.A. In general, burrowing owls nest in arid, open grasslands where they prey mainly upon arthropods (primarily insects), and small mammals (Glover 1953, Coulombe 1971, Thomsen 1971, Jaksić and Marti 1981). Population declines have occurred in recent decades throughout much of the

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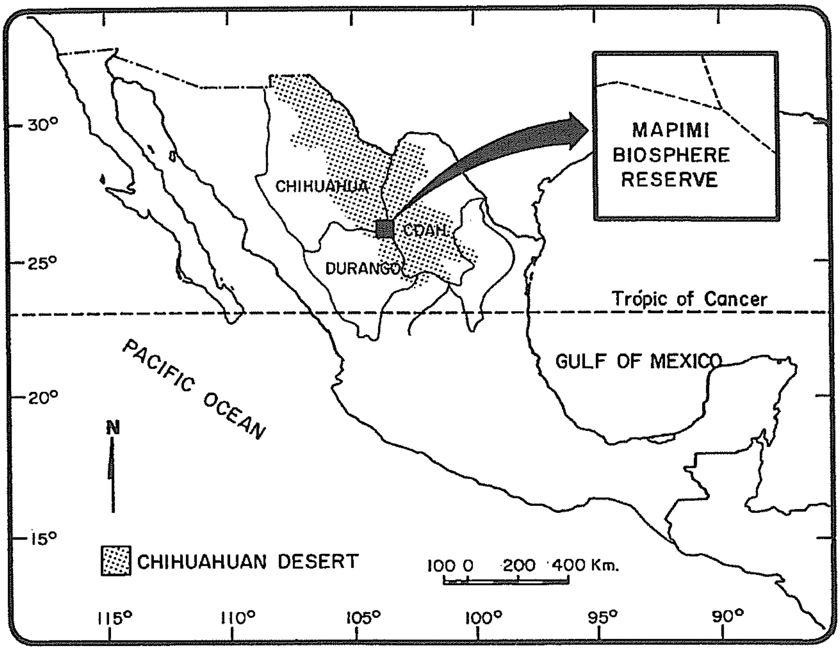

Figure 1. The Mapimí Biosphere Reserve study area.

owl's range, apparently due to habitat destruction and pest control of burrowing mammals (Best 1969, Butts 1973). This situation seems to be worsening as many contributions to this symposium have illustrated.

Very little information is available on the ecology of this species in Mexico (Rodríguez-Estrella 1993). The aim of this study is to present information on the habitat characteristics and feeding habits of the burrowing owl obtained during two breeding seasons in a northern desert of Mexico.

STUDY AREA AND METHODS

The owls were observed during 1985 and 1986 in 20,000 ha of the Mapimí Biosphere Reserve in the southern portion of the Chihuahuan desert (Fig. 1). Vegetation is a xerophilus scrub dominated by *Larrea tridentata, Fouquieria splendes, Prosopis glandulosa, Jatropha dioica, Agave* sp., *Opuntia* spp. and *Hilaria mutica*. Descriptions of the area may be found in Barbault and Halffter (1981). The study area elevation ranges from 1000–1350 m. The climate is arid-tropical with a mean annual temperature of 20.8°C, a mean monthly temperature ranging from 11.8°C in winter to 28.0°C during the summer, and an annual mean precipitation of 264 mm, with about 80% of the annual precipitation occurring during the summer. Livestock grazing is the principal human activity in the area, but habitat is still in good condition.

I located owls and their burrows from March through July in 1985 and 1986. Each week I monitored every burrow which appeared to be occupied by a pair, as indicated by the fresh lining of livestock or coyote dung around the entrance. For each occupied burrow I recorded the burrow type, the surrounding vegetation type, soil texture, number of suitable perches within 40 m of the burrow, distance to permanent water, and the distance to the nearest occupied burrow. Burrow types were classified according to the animal species that constructed them. Surrounding vegetation types were classified into seven minor habitat associations dominated by different plants. Soils were classified according to texture (Table 1). A Spearman correlation analysis was performed between the burrow characteristics and nesting success to determine relevant factors. Since the young were counted only after they started to fly during the post-fledgling period, it is possible that some counts underestimated the total number of fledglings per nest. Thus, I only considered a nest to be successful when fledglings were observed around the nest. Nests received a score of 1 if they were successful, and 0 if unsuccessful.

The feeding habits of the species were determined by analyzing pellets collected in and around the nests. The remains of prey in the pellets were identified to the highest possible level of taxonomic resolution of prey categories, generally species or genus level for vertebrates, and ordinal level for invertebrates. Mean prey weights were obtained from specimens directly trapped in the field and from the Universidad Autonoma Metropolitana (UAM, Mexico) collections. Mean prey size (MPS, $\bar{x} \pm$ S.E.) was calculated according to Herrera and Jaksić (1980). Prey diversity and food-niche breadth were estimated using the Shannon (H') and Levins (B) index,

Table 1. Burrowing owl nest site characteristics at the Mapimí Biosphere Reserve. *N* is the number of total nests and ($\%_{sn}$) represents the percentage of successful nests in 1985 and 1986.

	N	$\%_{sn}$
Vegetation type		
Larrea	4	25.0
Fouquieria-Larrea	8	62.5
Larrea-Prosopis-Agave-Fouquieria	13	46.1
Prosopis-Larrea	6	33.3
Prosopis	2	50.0
Prosopis-Hilaria	17	88.2
Fouqueria-Prosopis-Larrea	2	100.0
Total	52	
Soil texture		
Clay	18	50.0
Clay-sand	27	70.4
Sand	7	57.1
Total	52	
Burrow type		
Badger (*Taxidea taxus*)	11	72.7
Fox (*Urocyon cinereoargenteus*)	11	72.7
Kangaroo rat (*Dipodomys* spp.)	20	50.0
Coyote (*Canis latrans*)	1	0.0
Desert tortoise (*Gopherus flavomarginatus*)	9	66.7
Total	52	

respectively (see Krebs 1989). Evenness was calculated as J' = H'/H'max., where H'max. equals $\log_2$ of the total prey species (Pielou 1966). The numbers of prey species were used for computation of niche breadth. The MPS between years was compared by a Student's t test. Finally, a *t*-test was used to compare prey diversity (H') between years (Hutcheson 1970, Zar 1974).

RESULTS

I found 29 nesting pairs in 1985 and 23 pairs in 1986 in the Mapimí desert region. Nesting success was similar in both years (55% in 1985 and 65% in 1986), and nest failure was mainly due to the abandonment of burrows, although predation by coyotes and badgers, and human interference occurred as well (Rodríguez-Estrella and Ortega-Rubio 1993). Of the burrows occupied in 1985, 55% were occupied again in 1986.

Vegetation type was the factor most correlated with nesting success (r_s = 0.33; P = 0.015; Spearman rank correlation coefficients). Most nests were under grassland *Prosopis-Hilaria* and *Prosopis-Larrea* vegetal associations (Table 1), and when I combined the data of both years, I found that nests located at the *Prosopis-Hilaria* grassland vegetation were the most successful. Owls used five kinds of burrows, but mainly those constructed by kangaroo rats (*Dipodomys merriami, D. nelsoni*), although some could also have been constructed by spotted ground squirrels (*Spermophilus spilosoma*) (Table 1). The occupied burrows were most frequently in clay and clay-sand soils, over 3 km from water ($\bar{x} \pm$ SD = 3806 ± 2625 m). The nests ranged between 0.03 and 4.1 km ($\bar{x} \pm$ SD = 1125 ± 1000 m) from the nearest neighboring nest and were frequently located in the lower slope of small hills (30%). The number of perches within 40 m around the nests ranged from 4–20 ($\bar{x} \pm$ SD = 11.8 ± 4.9) (Rodríguez-Estrella and Ortega-Rubio 1993).

A total of 184 and 111 pellets were analyzed in 1985 and 1986, respectively. Burrowing owls in Mapimí preyed upon a wide variety of invertebrates, mainly scorpions, arachnida, coleoptera, and orthoptera preys (Table 2, Appendix 1) as well as small mammals (*Dipodomys, Perognathus, Peromyscus*). The proportions of the groups (mammals, birds, reptiles and invertebrates) in the diet of this owl were different between the two years (χ^2 = 19.2; df = 3; $P < 0.01$) as was the ingested biomass for each group (χ^2 = 979.0; df = 3; $P < 0.01$). Despite the greater proportion of invertebrates in the diet (85%), mammals represented >50% of the ingested biomass in both years. The MPS was different between the years (t = 20.01; df = 3541; $P < 0.01$; Table 2), due to a higher predation on reptiles in 1985. The mean number of prey per pellet was not different between years (t = 0.07; df = 293; $P > 0.05$; Table 2). Trophic diversity (H') was similar in both years (t = 1.14; df = 197; $P >$ 0.05), showing a relatively high prey diversity, but moderate evenness (J') (Table 2). The moderate evenness values indicate that *S. cunicularia* in Mapimí consume a relatively diverse array of prey species in relatively even proportions.

DISCUSSION

In the Mapimí desert, the burrowing owl is a common resident species throughout the year. In this region, they nest in open grassland habitats called "playas," much as they do in other North American deserts. They particularly nested where elevated perches were available and where their nests were mainly associated with a mixture of grassland vegetation and sparse trees (Rodríguez-Estrella and Ortega-Rubio 1993).

Table 2. Feeding habits of burrowing owls in Mapimí, Mexico. %P = percentage of the total number of prey; %B = percentage of the total ingested biomass (see Appendix 1).

	1985		1986	
PREY	%P	%B	%P	%B
Mammals	8.9	52.9	8.6	50.9
Birds	1.1	6.3	2.8	18.2
Reptiles	4.6	27.1	3.2	12.2
Invertebrates	85.5	13.7	85.4	18.7
Total number of prey & biomass[a]	2350	12 179.3	1193	5542.1
No. of pellets	184		111	
H′	2.35		2.13	
J	0.61		0.62	
B	8.03		5.45	
No. prey species	59		48	
No. pf prey/pellet	11.9 ± 11.4		11.8 ± 6.9	
MPS*	7.8 ± 4.1		5.2 ± 2.5	

[a] Biomass is given in grams.

The tendency of owls to nest in "playas" with the *Prosopis-Hilaria* association seems to be enhanced by the high availability of burrows, fine soil texture (clay-sand), number of perches, low nest predation, and availability of prey. All these factors may improve the reproductive success of burrowing owls in the *Prosopis-Hilaria* association (Rodríguez-Estrella and Ortega-Rubio 1993).

Burrowing owls in Mapimí used four types of mammal burrows as well as desert tortoise (*Gopherus flavomarginatus*) burrows. Frequently, these burrows were located in the lower portion of small hills where they offered a good horizontal visibility to the owl, possibly to avoid predation by mammals (Green and Anthony 1989, 1993).

At Mapimí a clay-sand soil texture seems to be the principal factor influencing burrow reuse, probably because it increases the longevity of a burrow (Morafka et al. 1981, Rodríguez-Estrella 1993). However, burrow reuse in Mapimí may also be related to low nest predation and to successful breeding in the previous year (or years). In this case, fourteen of 21 successful nest-burrows in 1985 were reused in 1986.

The prey of burrowing owls in Mapimí consisted mainly of insects and small mammals, similar to their diet in other areas (Coulombe 1971, Thomsen 1971, Jaksić and Marti 1981, Johnsgard 1988). These prey were especially abundant in the *Prosopis-Hilaria* association (Grenot and Serrano 1981, Thiollay 1981, Rodríguez-Estrella 1993).

The proportion of prey at the class level in Mapimí is similar to the diet of *Speotyto* in other areas of the U.S.A. (Fig. 2). As in other areas, this owl fed mainly on small prey. By numbers, invertebrates are the most common prey in all regions, but vertebrate prey are the most important prey in terms of biomass. However, some differences were noted between regions in both the occurrence of prey and ingested biomass. For example, in California, the occurrence of mammals in the diet of *Speotyto* appears to be more important than in other regions (Fig. 2a), but in terms of biomass, mammals were more important in Colorado (Fig. 2b). Reptiles were more important in the diet of burrowing owls in Mapimí compared to other regions (Fig. 2b) and its diet showed the highest reported prey diversity (H′) throughout its distribution (see Thomsen 1971, Jaksić and Marti 1981). The differences in the diet between regions seem to be related to regional differences in prey abundance and availability (Marti 1974, Jaksić and Marti 1981, Rodríguez-Estrella 1993).

Results of this work may lend support to the hypothesis that general features of predation by vertebrates exist in hot arid environments. Donázar et al. (1989) found that the diet of the great horned owl *Bubo virginianus* in North American deserts was related mainly to the presence of reptiles and arthropods. Hernández et al. (1994) concluded that the major role of reptiles and invertebrates as prey in the diet of coyotes (*Canis latrans*) in arid eco-

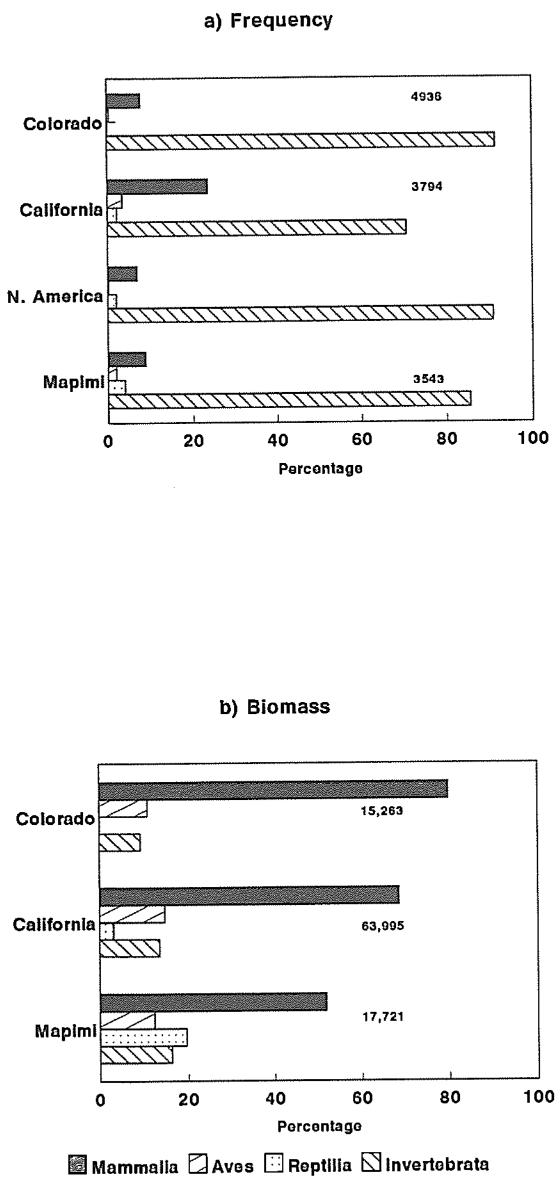

Figure 2. Percentage of prey categories in the diet of *Speotyto* in Colorado (Marti 1974), California (Thomsen 1971), North America (Johnsgard 1988) and Mapimí (this study). The numbers over the bars indicate (a) the total number of prey and (b) the total biomass in grams.

systems may be a characteristic feature of their trophic webs because of the high species density and abundance of these groups resulting from increased insolation. My results indicate similar trends in the use of reptiles and arthropods by the burrowing owl in the hot desert of Mapimí.

Cattle raising is one of the potential causes for the loss of burrows for the owl (Howie 1980), and in Mapimí, this human activity is the most important economic activity. During the study I observed several burrows destroyed by cattle. Thus, studies on the effects of cattle density on the breeding success of the burrowing owl should be conducted in order to determine the real effect of this activity on the owl population.

Finally, important changes in land use are expected over the next few years in many parts of Mexico as a result of the recent Trade Agreement (NAFTA) between Mexico, Canada and the U.S.A. The NAFTA will surely pressure a change in natural resource management in Mexico; i.e., the practices of the cattle industry. Thus, management plans should consider competitive economic practices with the least biological effects to ensure the conservation of Mexico's natural resources.

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Appendix 1. Burrowing owl diet in the Biosphere Reserve of Mapimí, Durango, Mexico in 1985 and 1986. The totals show the number of individuals per group and the ingested biomass in grams.

	WEIGHT (g)	1985		1986	
		% FREQ.	% BIOM.	% FREQ.	% BIOM.
Mammalia					
Lepus californicus juv.	300	0.30	17.24	—	—
Sylvillagus audubonii juv.	300	—	—	0.18	10.83
Spermophilus spilosoma					
adult	95	0.38	7.02	0.18	3.43
juvenile[g]	50	0.76	5.50	0.81	6.50
Thomomys umbrinus					
litter	40	0.09	0.66	—	—
Dipodomys merriami					
adult	37	0.21	1.52	0.45	3.43
juvenile	18.5	0.51	1.22	0.09	0.33
Dipodomys nelsoni					
adult	80	0.04	0.66	—	—
juvenile	40	—	—	0.09	0.72
Dipodomys sp.					
adult	40	—	—	0.45	3.61
juvenile	20	—	—	0.18	0.72
Perognathus penicillatus					
adult	15	1.62	4.68	1.17	3.52
juvenile[a]	10	0.13	0.16	0.99	1.17
Perognathus baileyi	15	0.09	0.25	0.27	0.81
Perognathus spp.					
adult	12	0.26	0.62	0.45	1.35
juvenile[a]	5	0.13	0.16	0.09	0.09
Neotoma albigula juvenile	90	—	—	0.09	1.6
Onychomyis torridus	14.5	0.13	0.36	—	—
Peromyscus eremicus					
adult	20	0.68	2.63	1.26	5.05
juvenile[a]	10	0.26	0.44	0.18	0.30
Reithrodontomys megalotis					
adult	15	0.30	0.86	0.36	1.08
Sigmodon hispidus					
juvenile	55	0.13	1.35	—	—
Mus musculus					
adult	18	0.68	2.36	—	—
juvenile[a]	9	0.04	0.04	—	—
Rodentia, unidentified					
adult	18	1.57	4.43	1.53	5.52
litter	5	0.09	0.10	0.36	0.36
Total[b]		208	6439.7	103	2821.1
Aves					
Callipepla squamata	189	—	—	0.09	3.41
Zenaida asiatica	152	—	—	0.09	2.74
Caprimulgidae	57	0.04	0.47	—	—
Myiarchus tyrannulus	27	0.04	0.47	0.09	0.49
Campylorhynchus brunneicapillus	50	0.90	0.66	—	—
Mimus polyglottos	53	0.17	1.36	—	—
Toxostoma curvirostre	50	—	—	0.09	0.90
Polioptila melanura	8	0.04	0.07	—	—

Appendix 1. Continued.

	WEIGHT (g)	1985		1986	
		% FREQ.	% BIOM.	% FREQ.	% BIOM.
Carpodacus mexicanus	21	0.04	0.17	—	—
Unidentified	20	0.55	2.13	2.61	10.65
Unidentified	50–100	0.09	1.23	—	—
Total		25	769	33	1008
Reptilia					
Scaphiopus couchi	17	0.34	1.12	0.63	2.15
Cophosaurus texanus	20	0.13	1.23	0.09	0.90
Holbrookia maculata	20	0.13	1.23	—	—
Scleoporus undulatus	10	1.32	2.55	1.44	2.89
Phrynosoma cornutum	36	0.72	5.02	0.18	1.30
Cnemidophorus inornatus	15	0.55	5.34	—	—
Cnemidophorus scalaris	20	0.26	2.46	0.09	0.90
Unidentified lizards	15	0.04	0.12	—	—
Masticophis sp.[c]	300	0.43	3.69	0.45	1.89
Pituophis melanoleucus[c]	280	0.17	1.31	0.18	0.72
Unidentified snakes	20	—	—	0.36	1.44
Unidentified snakes	100	0.09	1.23	—	—
Total		109	3303	38	676
Invertebrata					
Scorpionida	2	6.68	2.58	8.65	3.46
Arachnida	1	4.68	0.90	7.39	1.48
Solifugae	1	3.11	0.60	4.23	0.85
Chilopoda	5.0	0.21	0.21	—	—
Coleoptera	0.5	3.45	0.33	7.48	0.75
Meloidae	0.5	0.04	tr	0.09	0.01
Carabidae	0.5	1.11	0.11	4.23	0.42
Scarabaeidae	0.5	6.51	0.63	4.68	0.47
Phyllophaga	0.5	1.96	0.19	8.20	0.82
Diplotaxis	0.5	0.17	0.02	0.27	0.03
Elateridae	0.5	0.04	tr	0.18	0.03
Tenebrionidae	0.5	2.26	0.22	0.27	0.03
Curculionidae	0.5	0.38	0.04	0.81	0.08
Orthoptera	1.5	0.04	0.01	—	—
Gryllidae	1	17.02	3.28	30.45	6.10
Acrididae	2	5.23	2.02	2.97	1.19
Phasmatodea	1	0.17	0.03	0.09	0.02
Formicidae	—	27.70	0.53	6.58	tr
Hymenoptera	1	1.91	0.37	0.27	0.05
Vespidae	4	2.21	1.43	3.15	2.53
Dermoptera	2	0.13	0.05	0.27	0.11
Lepidoptera	1	—	—	0.09	0.02
Unidentified	1	0.26	0.05	1.44	0.29
Total		2008	1667.6	1019	1037.0
Grand Total		2350	12179.3	1193	5542.1

[a] Including litter of the prey.
[b] Totals represent the number of prey and the biomass (g) for each animal class.
[c] Individuals of different weights (20, 30, 60, 100 g).

MANAGEMENT AND RELATED SUBJECTS

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RECOVERY PLAN FOR THE BURROWING OWL IN CANADA

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ABSTRACT.—The population of burrowing owls, *Speotyto cunicularia,* nesting in Canada has been in decline since the mid-1900s and was classed as Threatened in 1978. The burrowing owl was extirpated from British Columbia, where it is now being reintroduced, and has experienced major declines across Manitoba, Saskatchewan, and Alberta. Habitat loss is considered a significant cause of decline although increased mortality from pesticides, vehicle collisions and unknown causes, (including mortality outside of Canada on migration and winter areas) are also of concern. Low productivity may also be contributing to the population decline. A National Recovery Plan for the burrowing owl, approved in December 1992, included these seven major strategies: Reduce mortality on the breeding grounds, increase productivity, protect and manage nesting habitat, monitor populations, manage migration and wintering areas, conduct release programs, and develop public support.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *Canada; Recovery Plan.*

Plan de recuperacion del tecolotito enano en Canada

RESUMEN.—La poblacion de tecolotito enano, *Speotyto cunicularia* que anida en Canada a disminuido desde mediados de los 1900s y se clasifico como amenazado en 1978. El tecolotito enano se extirpo de British Columbia donde actualmente se trata de reintroducir, y ha sufrido grandes bajas atraves de Manitoba, Saskatchewan y Alberta. Perdida del habitat se considera una causa significante en las bajas, aunque aumento en la mortlidad a causa de pesticidas, choques con vehiculos y causas no conocidas (incluyendo mortalidad fuera de Canada en migracion y areas invernales) tambien son de considerar. Baja productividad tambien puede estar contribuyendo a las bajas de la poblacion. Un plan nacional de recuperacion para el tecolotito enano aprobado en diciembre de 1992 incluyo estas siete estrategias: Reducir mortalidad en areas de reproduccion, aumentar la productividad, proteger y manejar el habitat de anidacion, monitorear las poblaciones, manejar areas de migracion e invernacion, realizar programas de liberacion, y desarrollar apoyo publico.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl, *Speotyto cunicularia,* has been classed as a Threatened species in Canada since 1978. Canada appointed a National Burrowing Owl Recovery Team in 1989 and the National Recovery Plan for the Burrowing Owl (Haug et al. 1992) was approved in December 1992. With this paper, I briefly explain the burrowing owl's status in Canada, the reasons for its decline, and the recovery actions proposed in the recovery plan. I also stress that this migratory species spends six months outside of Canada. The species recovery in Canada therefore depends on international cooperation.

STATUS OF THE BURROWING OWL IN CANADA

The burrowing owl is found in the four western provinces of Canada: Manitoba, Saskatchewan, Alberta and British Columbia. Our most western population, in the interior valleys of British Columbia, had been extirpated, but a release program reestablished a small population, six pair in 1992 (Haug et al. 1992).

Our second population, estimated at about 2000 pairs (Haug et al. 1992) occupies the Canadian prairies from Alberta to Manitoba. Figure 1 shows that the range has contracted, especially on the eastern side, since 1978.

Our concern for the survival of this species arises from several studies which show precipitous declines in the population. James (1992a) reported declines of approximately 10% per year on his study area near Regina. Less than 10% of sites in the Saskatoon area occupied by burrowing owls in

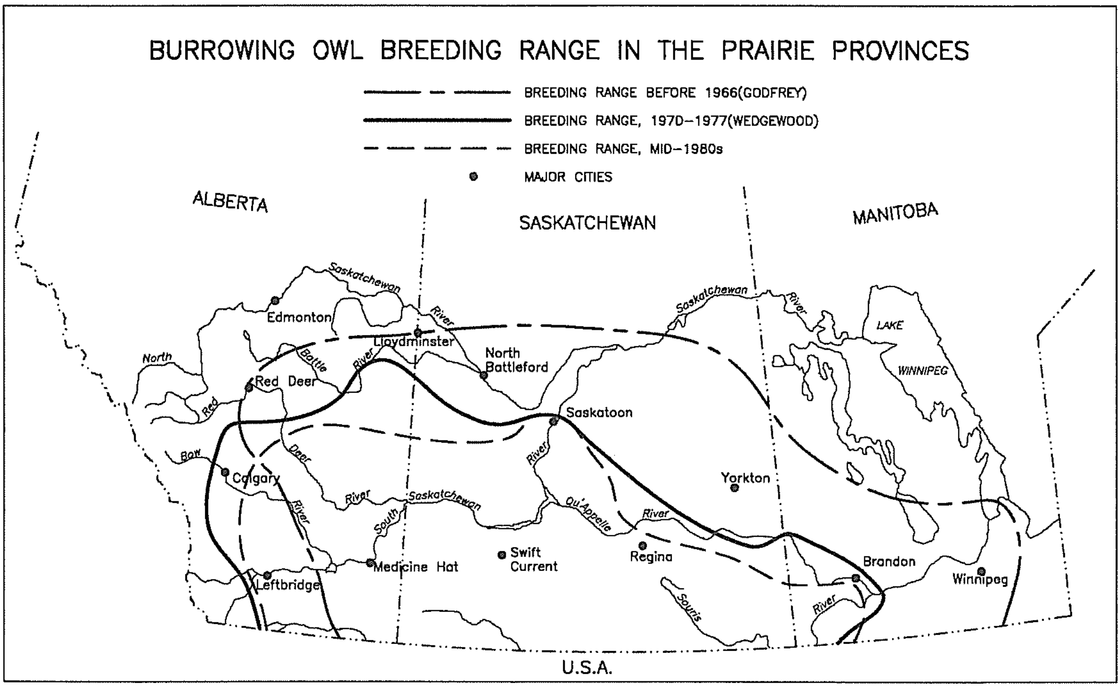

Figure 1. Burrowing owl breeding range in prairie Canada after Bjorklund (1992).

1975 (Wedgwood 1976) were still occupied by burrowing owls in 1992 (Wedgwood pers. comm.). The number of pairs reported breeding on Operation Burrowing Owl sites declined steadily from 721 in 1988 to 322 in 1993 (Dundas 1993). The Operation Burrowing Owl data is obtained by rechecking initially occupied sites and obtaining reports of new sites. Rechecking same sites creates a bias toward showing a decline (Rich 1984). However, if the observed population decline is simply due to movement between sites, a substantial number of new sites should be reported each year and old sites should eventually be reoccupied. That this is not occurring indicates the decline is real (Hjertaas 1992). In Manitoba the population has declined from 76 pairs in 1982 (Ratcliff 1986) to 28 pairs this year and the range has contracted into the southwest corner of the province (Haug et al. 1992).

Cause of the Decline. The causes of the decline are complex and interrelated. The National Recovery Team has identified loss, fragmentation and degradation of breeding habitat, mortality from collisions with vehicles, exposure to the pesticide carbofuran, and reduced productivity as contributing factors (Haug et al. 1992). Canadian burrowing owls may also experience problems on migration and wintering areas.

The Recovery Plan. The recovery goal is "To increase populations of the burrowing owl in Canada to a self-sustaining level such that the species is no longer considered Threatened or Endangered." This goal is elaborated in two objectives: to produce a stable or increasing population of more than 3000 pairs in the prairie provinces and to establish a viable population in British Columbia. Seven principal strategies were adopted to meet these objectives (Haug et al. 1992).

1. Reduce mortality on the breeding grounds

The principal mortality factors affecting burrowing owls include pesticide poisoning, collisions with vehicles, predation and occasional incidents such as shooting. A major strategy is to eliminate the negative effects of pesticides on burrowing owls. Although all pesticides, including rodenticides, are of concern, carbofuran is of greatest concern. Carbofuran is widely used in prairie Canada for grasshopper control, and its impacts on burrowing owls and their productivity when applied within 250 m of the nest burrow have been demonstrated (James and Fox 1987). Agriculture Canada has responded to this concern by imposing an interim label restriction preventing carbofuran application within 250 m of burrowing owl burrows while a final decision on relicensing carbofuran is pending. The effectiveness of this label is in doubt as many farmers are not aware of the restriction (Mufatov 1992).

Additional planned action is aimed at reducing collisions with vehicles, publicity and enforcement to prevent shooting, developing policy to resolve owl-human conflicts and research and monitoring of mortality rates and causes.

2. Increase productivity

Increasing productivity could help stabilize or increase the burrowing owl population. Research on nest predators, causes of differential productivity between areas, and the effect of food supplies on productivity is planned or underway.

Research conducted during 1992 suggests that food is limiting productivity (Wellicome 1992) and that habitat management to increase food supplies may be necessary to boost productivity in some areas. Food may be limiting because nests are commonly situated in heavily grazed pastures surrounded by intensively cultivated land. Neither of these habitats supports large numbers of microtines, a key food resource during the earlier parts of the breeding season.

3. Protect and manage nesting habitat

Unfortunately burrowing owls on the prairies tend to select potentially arable grasslands as nest sites. With the decline of the mixed farm and trend toward pure grain farming, nesting habitat has disappeared, leaving only small and fragmented habitats for the owls (Haug 1985, Hjertaas and Lyon 1987, Haug and Churchward unpubl. data). This fragmentation may increase predation and create other problems, such as the lack of foraging habitat just discussed.

The Recovery Plan calls for a series of actions to maintain critical nesting areas and essential habitat features such as nesting holes and foraging areas. The emphasis has been on landowner contact programs such as Operation Burrowing Owl. These programs are designed to create awareness and protect privately owned nesting areas (Hjertaas 1992) and will continue as part of an expanded effort to identify and protect critical nesting areas.

Many provincial and federal agricultural policies directly encourage and subsidize conversion of grassland to cultivation, thus reducing habitat available for burrowing owls and other species. The plan identifies this as a basic and urgent problem which must be resolved. Unfortunately, identifying the problems with these policies is easier than achieving a consensus for change.

The Recovery Plan identifies the need to expand from simple habitat protection to habitat management to ensure sites have the necessary habitat components, including adequate nest burrows and feeding areas.

4. Monitor populations

Assessing the effectiveness of any plan requires checking results against the goals and objectives. Monitoring actual population size across the prairies would be very expensive because the burrowing owl population is thinly spread over large areas. While a better understanding of habitat may eventually facilitate such surveys, the key to recovery on the prairies is a stable or increasing population. Except in British Columbia and Manitoba, where near total counts are feasible, monitoring will therefore focus on trend, mortality and productivity rather than on absolute numbers. Randomly chosen monitoring blocks have been established in Alberta and Saskatchewan to aid in tracking population changes.

5. Manage on migration and wintering areas

The winter range and migratory corridors of Canadian burrowing owls are not known. James (1992b) suggests the lack of band returns during winter indicates the prairie population migrates to Mexico. Band returns from the migration period (Fig. 2) indicate movement that could stop in the United States or continue into Mexico.

The importance of winter range to survival of the population makes locating and managing the winter range a key part of recovery. Continued banding studies, banding on wintering areas, and techniques such as genetic or chemical analysis or radiotelemetry will be used to identify wintering areas of Canadian burrowing owls. This work will be combined with surveys of possible wintering areas, especially in Mexico, to determine winter distribution of the burrowing owl.

The ecology and factors limiting survival of the burrowing owl during the migration and winter must also be determined. This work can proceed

Figure 2. Foreign recoveries of burrowing owls banded in Canada (modified from James 1992b) showing banding and recovery sites. Numbers indicate the month of recovery.

immediately. Even if research areas are not ultimately proven to harbor burrowing owls from Canada, the information gained will be useful in managing resident and other migratory populations.

Identifying migration and winter areas and studying the species during this period must be conducted cooperatively. If this research identifies substantial management problems, management to help the burrowing owl should also be cooperative. This approach could mean joint projects between members of our team and Mexican or American researchers. It may involve naming Mexican and American representatives to the Canadian Recovery Team. The Recovery Team is currently seeking possible partners for winter studies.

6. Conduct releases

Where populations of burrowing owls are very low, as in Manitoba, or absent, as was the case in British Columbia, releases offer what may be the only way to maintain or establish breeding populations.

7. Develop public support through education

Public awareness is even more essential for recovery of the burrowing owl than for many other threatened species because the species has frequent public contact. Nesting in intensively farmed areas, in towns and cities, and on private land makes it vulnerable to human interference, land use changes and pesticides. Actions necessary to help the burrowing owl recover will depend primarily on public goodwill and cooperation. Planned communication will promote specific programs and increase awareness of the burrowing owl. It will also address underlying issues in an attempt to communicate that problems with the burrowing owl are not unique, but symptomatic of our land use practices and general environmental degradation. As such, they cannot be dealt with in isolation, but as part of the larger realm of public policy.

CONCLUSION

In spite of recovery efforts, population declines are continuing, increasing our concern for this species. We will be actively implementing the plan and attempting to address the above issues.

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OPERATION BURROWING OWL IN SASKATCHEWAN

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ABSTRACT.—Operation Burrowing Owl was initiated in 1987 as a private stewardship program to protect burrowing owl, *Speotyto cunicularia,* habitat. Landowners with burrowing owls were asked to sign a voluntary agreement to preserve the nesting site for five years and to annually report the number of owls at the site. In return they would receive a gate sign and an annual newsletter. Eighty-five percent of eligible landowners did enroll when contacted. After five years 499 landowners had agreed to maintain a total of 16 000 hectares of grassland as burrowing owl nesting habitat. Numbers known to be nesting on these sites fluctuated from 721 in 1988 to 322 in 1993. Operation Burrowing Owl has protected habitat and substantially raised public awareness of the burrowing owl. Data collected through the program indicate a significant population decline is occurring. Other available data sources also indicate that populations declined since 1988.

KEY WORDS: *burrowing owl; Operation Burrowing Owl;* Speotyto cunicularia; *Canada; management; habitat; Saskatchewan.*

Operacion tecolotito enano en Saskatchewan

RESUMEN.—Operacion Tecolotito Enano fue iniciada en 1987 como un programa privado de administracion para proteger el habitat del tecolotito enano, *Speotyto cunicularia.* A terratenientes con tecolotito enano se les pidio firmaran un acuerdo voluntario para preservar el habitat de anidacion por 5 años y que anualmente reportaran el numero de tecolotes en el sitio. A cambio recibirian un anuncio para puerta y un boletin informativo anual. 85% de los terratenientes habian acordado mantener un total de 16 000 hectareas de pradera como habitat reproductivo des tecolotito enano. Numeros que anidaron en estos sitios variaron de 721 en 1988 a 322 en 1993. La Operacion Tecolotito Enano ha protegido habitat y ha elevado la conciencia publica sobre el tecolotito enano. Datos colectados durante el programa indican que una disminucion significante ha occurrido en la poblacion. Otras fuentes de informacion tambien indican que las poblaciones han disminuido desde 1988.

[Traducción de Filepe Chavez-Ramirez]

The majority of the arable land in Canada's prairie provinces is privately owned. Thus conservation initiatives in this landscape are largely dependent on cooperation between landowners and conservationists. One such cooperative program, Operation Burrowing Owl (OBO), operated in Saskatchewan since 1987 and now also operates in Alberta to protect privately-held grasslands used as nesting areas by the burrowing owl, a threatened species in Canada.

The need for a habitat protection program for the burrowing owl was demonstrated when Hjertaas and Lyon (1987) found that twenty-one percent of the grassland areas in southeastern Saskatchewan identified as potential burrowing owl nesting habitat had been cultivated or otherwise eliminated over the previous seven years.

Hjertaas and Lyon (1987) also learned that the burrowing owl was relatively rare: burrowing owls were located on only 13 of 703 grassland plots searched. However, comments from farmers whose land we searched suggested the burrowing owl had formerly been more common. Discussions with farmers also showed that most could identify a burrowing owl, but very few knew it was threatened or even uncommon.

In 1986 thirteen pairs of burrowing owls near Kronau, Saskatchewan, were threatened by the landowner's decision to cultivate the pasture they nested in. This colony was saved when the World Wildlife Fund (Canada) and the Saskatchewan Wildlife Federation agreed to pay the landowner $360.00 annually to retain the area as pastureland.

The above 1986 survey and the threat to the Kronau colony demonstrated an urgent need for a program to protect burrowing owl habitat. They also showed the potential for a cooperative program to raise awareness of the burrowing owls' threatened status and to be an effective conservation force. In 1987, OBO was initiated as a joint project of the Saskatchewan Natural History Society, Saskatchewan Wildlife Federation, World Wildlife Fund, Wildlife Habitat Canada and Saskatchewan Environment and Resource Management with the following objectives: (1) to protect burrowing owl habitat by publicly recognizing the landowners' role in providing habitat; (2) to survey burrowing owl populations across Saskatchewan and estimate provincial and regional populations; (3) to increase public awareness that the burrowing owl is a threatened species; (4) to establish a method for annual census of the owl population on protected habitat; and (5) to facilitate research.

METHODS

The core of OBO is a one-page volunteer agreement which OBO staff discuss and sign with landowners who have burrowing owls on their property. The OBO partners agree to provide the landowner with an OBO sign (with the landowners name), which is designed to be placed at the farm gate, and an annual newsletter about burrowing owls. The participating landowners agree not to cultivate the described nesting area for the five-year term of the agreement and to report the number of pairs of burrowing owls annually when requested to do so. This agreement is essentially a handshake agreement which can be cancelled at any time and is not legally enforceable.

At the start of this program the location of the majority of our burrowing owl colonies was unknown. Thus, to meet the objectives of raising awareness and surveying populations, and also to find landowners with whom we could sign agreements, we initiated a publicity program. Our key message was ". . . the burrowing owl is a threatened species which needs help. If you know where they nest please tell us." This message was initially sent to every rural post office box holder within the burrowing owl's Saskatchewan territory with a simple mail-back questionnaire.

The initiation of OBO received a substantial boost from the International President of the World Wide Fund For Nature, His Royal Highness Prince Philip, who participated in a formal initiation of the program. Eight landowners from across the province were enrolled in the program and received their OBO signs from the Prince. In addition to excellent coverage in the provincial media, almost every one of the widely read rural weekly papers ran the OBO story on their front page, using photographs provided by OBO of someone from their region with H.R.H. Prince Philip. In 1992 the Prince again assisted the program by writing a thank-you letter to renewing members.

Since the 1987 initiation we have attempted to keep OBO in the pubic eye through the use of a brochure, by giving presentations to schools and groups and by placing occasional stories in the media. A toll free "HOOT LINE" was introduced in 1991 to allow people to report sightings or census results at no cost to themselves.

Ongoing contact with the cooperating landowners via the OBO Newsletter and the owl population survey is an important part of OBO. This contact has three purposes: (1) to reinforce the message that the burrowing owl is threatened and maintenance of nesting sites is vital; (2) to obtain population data annually; and (3) to provide information on safer practices (e.g., on the use of pesticides). Personal contact and inspection of the nesting areas by OBO staff occurred primarily at the sign-up and again, after 5 years, when the agreements were renewed. Landowners appeared to take pride in showing OBO staff their burrowing owl site and usually enrolled immediately. Occasionally, personal contact could not be made and contacts with the landowner were limited to mail and telephone. Such contacts were less successful in enrolling members than personal contacts.

Nest boxes for burrowing owls were placed on a series of OBO sites. Experience has shown that, except for special situations like golf courses, adequate natural holes were available for nesting on most OBO sites, but nest boxes were valuable in increasing landowner interest, encouraging owls to nest in safer areas, (such as at the edge instead of on a ball diamond) and in facilitating banding and other research.

RESULTS

OBO staff noted a dramatic increase in awareness of the burrowing owl as a threatened species following the mailing to landowners and the widespread media coverage of H.R.H. Prince Philip inaugurating the program. The OBO intent, that people who had burrowing owls would value them as something special, was achieved in many cases. This change in awareness and attitude was very noticeable during contacts to enroll landowners. The OBO gate signs (which 75% of members have erected) and the continuing publicity by OBO as well as promotion by the landowners themselves, have helped maintain awareness of the burrowing owl since 1987. Nonetheless, some landowners remain unfamiliar with the program: in 1992 82% were familiar with the burrowing owl while only 62% reported familiarity with Operation Burrowing Owl.

During the initial five years, 499 landowners, ranging from individual farmers to the city of Moose Jaw, enrolled 16 000 ha of grassland nesting habitat in OBO. Eighty-five percent of the landowners, who had burrowing owls and were eligible for the program, did enroll when contacted. The remaining 15% were either not interested in burrowing owls or did not want to become involved in what they perceived as another government program.

Beginning in 1992, we sought to re-enroll the landowners whose 5-year agreements were expiring. Two hundred and eighty-six of the 356 members did enroll for an additional 5 years even though only 46% of them still had burrowing owls nesting on their property. Those who no longer had burrowing owls were convinced that keeping the habitat is essential to hopes for a recovery in the population. New agreements have just balanced dropouts and maintained the membership in 1993 at the 499 achieved in 1991.

Data collected during the 1993 census of the burrowing owl on OBO sites indicated that the grassland habitat originally enrolled in the program remained on 98.1% of sites although cessation of grazing may have reduced the attractiveness of 6.8% of the sites to nesting burrowing owls (Dundas 1993). Only 1.9% of landowners had already or were planning to cultivate areas enrolled in OBO. No direct comparison with this rate of loss of grassland habitat is available. However, data from the national census show 3.76% of the "unimproved" land (i.e., native ecosystem) in agricultural Saskatchewan was "improved" for agriculture between 1986 and 1991 (Ted Weins pers. comm.). Improved for agriculture usually means cultivated. Because much of the "unimproved land" in agricultural Saskatchewan is not suitable for cultivation, the rate of conversion on potentially arable lands, which includes almost all OBO sites, would have been significantly higher than 3.65%. This suggests that OBO is having a positive affect on maintenance of burrowing owl habitat. OBO has given us a list of known nesting areas and a known minimum population size, but the accuracy of provincial population estimates is limited by the unknown number of unreported sites.

The trend in population numbers is perhaps more important than the absolute number of burrowing owls. The annual reports from landowners have provided an opportunity to track the population trend. Unfortunately, this method of collecting data creates possible biases from count accuracy, low reporting rates and annual movement of owls.

We believe the count accuracy is reasonable for small colonies. Only a small number of sites supported more than five pairs of nesting owls where landowners may be confused about the number of pairs. For example, Table 1 shows that in 1992 the most common nesting situation was a single pair, with more than half the population in colonies of one, two or three pairs. We have attempted to verify larger colony counts by personal visits.

Table 1. Size of burrowing owl colonies on Saskatchewan Operation Burrowing Owl sites in 1992 with total number and percentage of pairs inhabiting colonies of each size (modified from Bjorklund 1992).

No. of Pairs in Colony	No. of Colonies	Total No. of Pairs	% of All Pairs
1	112	112	20.9
2	56	112	20.9
3	20	60	11.2
4	19	76	14.1
5	9	45	8.4
6	6	36	6.7
7	4	28	5.2
9	1	9	1.7
10	1	10	1.8
14	2	28	5.2
21	1	21	3.9

A second bias is created because not all members responded to questionnaires on population numbers in 1988, 1989 and 1990. In 1991 a policy of telephoning to obtain late reports, better designed and postage-free reporting cards and a draw for gift certificates for reporting members produced reporting rates of 95% or greater. The lower response rates for those three years probably lowered the total number of owls reported and may bias the number of owls per member upward since participants who had owls may be more likely to submit survey reports.

The final possible bias in the OBO data set arises because it starts with known occupied habitats. Rich (1984) showed there was enough movement between burrows that simply rechecking used burrows is inadequate to monitor populations. Although the Operation Burrowing Owl data is based on blocks of land, usually pastures rather than individual burrows, some bias should exist. Thus, a decline is expected on existing sites even if the provincial population is stable.

The number of owls reported from OBO sites has declined substantially (Table 2) since 1991 while the number of pairs per reporting member has declined since 1988.

If the population is stable the decline in owl numbers at previously occupied sites should be at least partially offset by new enrollments and abandoned sites should be reoccupied after a period of time (Rich 1984). If only half of the 62% of landowners familiar with OBO reported new sites, one

Table 2. The number of pairs of burrowing owls reported by Operation Burrowing Owl (OBO) members, the number of members from whom reports were received and an index of pairs per reporting member from 1987 to 1993 (Dundas 1993).

	No. Owl Pairs	No. Members Responding	OBO Pair Index
1987	600	265	2.26
1988	721	232	3.11
1989	657	221	2.97
1990	467	265	1.76
1991	647	497	1.30
1992	561	482	1.16
1993	322	473	0.68

third of all new sites in the province would be reported. Actual reporting rates should be higher, because people do report burrowing owls they observe on other peoples' land, and landowners who are unfamiliar with Operation Burrowing Owl may nonetheless know the burrowing owl is threatened and report observations to conservation officers. However, in 1993, when the reported population on existing sites declined by 239 pairs, only 11 new members were enrolled. In addition, almost all abandoned OBO sites are remaining unoccupied.

The other data sources available all confirm the population decline shown by OBO. The population on Paul James' study area near Regina has declined from 78 pairs in 1987 to 18 pairs in 1993 (Paul James pers. comm.). Naturalists at Saskatoon report that they can no longer find burrowing owls near that city (Stan Shadick pers. comm.), and other naturalists have also noted declines.

More traditional randomized surveys to confirm the population status and trend have been difficult and expensive. In 1994, Saskatchewan Environment and Resource Management employees attempted to address the issue of bias by establishing randomly selected population monitoring blocks in suitable habitats. Thirty-four days of search effort discovered three pairs of burrowing owls (Earl Wiltse pers. comm.). A survey which would produce statistically valid numbers would clearly be very expensive.

Conclusion

A private stewardship program such as OBO has limitations, but has been successful in creating awareness and enlisting broad support for burrowing owl conservation. Most importantly, it has established a network of cooperative and concerned landowners who are willing to retain and, in some cases, even manage grassland habitat for burrowing owls. The vast majority of landowners honored their agreements and maintained the nesting habitat even if the owls were no longer present. General public awareness of the burrowing owl has increased dramatically since 1987. One side benefit of this awareness is that burrowing owls threatened by road, pipeline or other development are now reported to OBO or the Saskatchewan Environment and Resource Management so conflicts can be resolved without harm to the burrowing owls.

The OBO data set does provide the best data available on population trends of this species in Saskatchewan. The program now achieves a high level of reporting from its members, thus the value of the data for population monitoring will increase in the future. While the data contains an inherent bias because it begins with occupied sites, reoccupancy rates and new sign-ups provide a check on whether declines are real or due to that bias. One advantage of this method of population monitoring is that land-owner cooperation allows sampling of a substantial portion of the provincial population at a low cost.

The success of OBO has depended to a great extent on individual contact. The personal visit was remembered and has provided strong reinforcement of the importance of that site for nesting burrowing owls. Maintaining or increasing a level of personal contact will be essential to the continuing success of this program.

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ECOLOGICAL CONSIDERATIONS FOR MANAGEMENT OF BREEDING BURROWING OWLS IN THE COLUMBIA BASIN

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ABSTRACT.—Burrowing owl (*Speotyto cunicularia*) nest-site selection in the Columbia Basin appears to be based largely on the availability of potential nest burrows, vegetation structure, and food sources immediately adjacent to the burrow. Burrowing owls inhabiting the Columbia Basin of Oregon and Washington rely largely on badgers to excavate nest burrows (Green and Anthony 1989). However, badgers are also a major predator of burrowing owl nests (Green and Anthony 1989). To avoid badger predation by early detection, burrowing owls in the Columbia Basin tend to select burrows surrounded by either very short (≤5 cm) vegetation or a variety of elevated perches that provide good horizonal visibility around the nest site. They also appear to avoid nesting in shrub habitats where the average shrub coverage is >15%. In addition, burrowing owls often line their nest burrows with livestock dung, presumably to mask odors of nest occupants from potential mammalian predators. Burrowing owls also tend to select burrows surrounded by a high percentage ($\bar{x}$ = 55%) of bare ground, where prey (Heteromyid rodents and ground-dwelling arthropods) populations are presumably high.

Abandonment of nest sites tends to occur when distances between nest sites are less than 110 m, an important consideration when positioning artificial nest boxes. Furthermore, small nest boxes can become overcrowded by growing broods, often forcing movements of part of the brood to auxiliary burrows, potentially increasing the susceptibility of nestlings to predation or abandonment. Therefore, several aspects of burrowing owl nesting ecology, including predator avoidance, intraspecific competition, prey selection, and brood development, should be understood before designing a program for managing nesting habitat in a given area. In this paper we discuss nesting ecology and provide recommendations for managing populations of burrowing owls nesting in the Columbia Basin.

KEY WORDS: *burrowing owl*; Speotyto cunicularia; *management*; *Columbia Basin*; *Oregon*; *Washington*; *nest box*; *nesting*.

Consideraciones ecologicas para el manejo del tecolotito enano que se reproduce en Columbia Basin

RESUMEN.—La seleccion de sitios de anidamiento por el tecolotito enano (*Speotyto cunicularia*) en Columbia Basin parece estar basada en la disponibilidad de nidos madriguera, estructura de la vegetacion y fuentes de alimento adyacentes a la madriguera. Los tecolotitos enanos que habitan el Columbia Basin de Oregon y Washington dependen principalmente del tejon para que excave las madrigueras de anidar (Green y Anthony 1989). Sin embargo, el tejon es un principal depredador de nidos de tecolotito enano (Green y Anthony 1989). Para evitar depredacion por el tejon en base a pronta deteccion los tecolotitos enanos en Columbia Basin tienden a seleccionar madrigueras rodeadas por vegetacion corta (<5 cm) o una variedad de perchas elevadas que provean buena visibilidad horizontal alrededor del sitio del nido. Tambien parecen evitar anidar en habitats arbustivos donde la cobertura promedio de arbustos es > 15%. Ademas los tecolotitos enanos regularmente forran sus madrigueras con heces de ganado supuestamente para enmascarara los olores de los ocupantes del nido a los mamiferos depredadores. El tecolotito enano tiende a seleccionar madrigueras rodeadas por alto porcentaje ($\bar{x}$ = 55%) de suelo descubierto donde las poblaciones presa (roedores Heteromyide y arthropods de suelo) son presuntamente altas.

Abandono de nidos tiende a ocurrir cuando la distancia entre sitios de anidacion son menos de 110 m, una importante consideracion cuando se van a situar cajas artificiales de anidacion. Cajas chicas pueden sobrecargarse por las crecientes crias forzando movimientos de parte de la nidada a madrigueras auxiliares, potencialmente incrementando la susceptibilidad de los pollluelos a depredacion o abandono. Varios aspectos de la ecologia de anidacion del tecolotito enano incluyendo evitar depredadores,

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competencia intraespecifica, seleccion de presas, y el desarrollo de la nidada deben de comprenderse antes de diseñar un programa de manejo para habitat reproductivo en un area determinada. En este escrito discutimos ecologia reproductiva y damos recomendaciones para el manejo de poblaciones del tecolotito enano que anidan en Columbia Basin.

[Traducción de Filepe Chavez-Ramirez]

Management of wildlife habitat requires information on habitat selection and potential impacts to habitats important to the species of concern (Brown and Curtis 1985). Since Zarn (1974) suggested that burrowing owls (*Speotyto cunicularia*) require burrows surrounded by short, open vegetation, few authors (e.g., Craig 1974, Collins and Landry 1977, Andersen 1989, Haug and Oliphant 1990) have provided direct recommendations for managing burrowing owl habitat. Furthermore, no specific habitat management recommendations have been developed for burrowing owls breeding in the Columbia Basin region of Oregon and Washington. Finally, the unique ecology of this region (early rainfall patterns and lack of large, colonial sciurids), and this owl population's dependency on the badger (*Taxidea taxus*) for nest burrows (Green and Anthony 1989), suggest that management recommendations from elsewhere in the range (especially where owls depend on colonial sciurids for providing nest burrows) may not fully apply.

Herein, we describe several aspects of the nesting ecology of Columbia Basin burrowing owls, including predator avoidance, intraspecific competition, brood development, and prey selection, and present habitat management recommendations based on this information.

Ecological Considerations

Several aspects of burrowing owl nesting ecology should be understood before designing a successful program for managing nesting habitat. Four of these aspects are the need to: (1) avoid predation; (2) avoid competition, especially with conspecifics; (3) meet the shelter demands of a large, growing brood; and (4) obtain an adequate food supply. The challenge in managing habitat for breeding burrowing owls is to recognize whether any of these needs are lacking and then to rectify, where possible, these inadequacies through manipulation or preservation techniques.

Predator Avoidance. A universal component of burrowing owl nest habitat is a burrow surrounded by short vegetation (Butts 1971, Coulombe 1971, Zarn 1974, MacCracken et al. 1985, Rich 1986, Green and Anthony 1989). Presumably, this lack of vegetation allows both adults and nestlings a commanding view of their surrounding environment and the ability to detect an approaching predator early enough to escape. Short vegetation is naturally found in prairie dog (*Cynomys* spp.) towns (Bonham and Lerwick 1976, Hansen and Gold 1977, Knowles et al. 1982) and this is probably why, besides burrow availability (Zarn 1974), prairie dog towns attract burrowing owls. Green and Anthony (1989) found that Columbia Basin burrowing owls nest successfully in grassland areas where the average vegetation height was <15 cm, but further found that when the average vegetation height was 5–15 cm, burrowing owls always selected a burrow with a nearby elevated perch. Green and Anthony concluded that the elevated perch allowed male burrowing owls to remain vigilant to approaching predators even after daytime soil surface temperatures became intolerably hot for standing on the ground. This is especially important if burrowing owls use their legs as heat dissipators as suggested by Coulombe (1971). Butts (1971) also noted that burrowing owls using badger burrows in Oklahoma nested within 90 m of a fence (i.e., a perch). Green and Anthony further concluded that an elevated perch was not necessary if the surrounding vegetation was short enough (≤5 cm) to allow the male a commanding view while peering over the lip of the burrow and keeping his legs in the burrow shade, a common surveillance posture at very short vegetation nest sites. Consequently, providing artificial perches may enhance burrowing owl nesting habitat in grassland areas where burrows and vegetation averaging <15 cm are present but natural perches are lacking. Our observations (unpubl. data) have shown that these perches can be as low as 20 cm, although when given several choices, burrowing owls preferred to perch at 1–2 m heights.

Habitats dominated by large, woody shrubs such as bitterbrush (*Purshia tridentata*) or big sagebrush (*Artemisia tridentata*) generally have an abundance of suitable perch sites (structurally stable shrubs). Green and Anthony (1989) suggested that one reason burrowing owls may have avoided rabbitbrush- (*Chrysothamnus* spp.) dominated habitats in their study area was because of the inability of these shrubs to support the weight of a perching owl. However, perch availability aside, Green and Anthony found owls to select shrub habitats where shrub volumes and coverage were considerably less than average, which may indicate a trade-off between maximizing view-enhancing perch numbers and minimizing the number of view-obstructing shrubs. In Green and Anthony's study 89% of the nest sites in shrub habitats occurred where shrub cover was <15%. We suggest using the 15% shrub cover value as a cut-off when selecting shrub habitats for managing for nesting burrowing owls.

Green and Anthony (1989) tested Martin's (1973) hypothesis that burrowing owls line their nest and tunnel entrance with cattle dung in order to avoid mammalian predators by masking nest odors. Of 15 nests lost to predation during one year of their study, only two (13%) were lined with dung. In contrast, of 32 nests which were successful, 23 (72%) were lined. Although their results do not fully conclude that cattle dung is a strong deterrent to mammalian predation, the evidence is compelling enough to warrant providing dung to nesting owls if not already available as a management consideration, especially if badgers occur in the area.

Intraspecific Competition. Burrowing owls nesting in large sciurid colonies are commonly found nesting in close proximity (<100 m) with apparently high nesting success (Butts 1971, Thomsen 1971). However, in the Columbia Basin, we found a high frequency of nest desertion when two pairs nested within 110 m (Green and Anthony 1989). We attributed this phenomena to competition by neighboring pairs over insect prey. This competition does not generally manifest itself until midway into the nesting cycle (late May to early July) when the owl's primary rodent prey, Great Basin pocket mice (*Perognathus parvus*) (Green et al. 1993), shift their activity underground in response to the Columbia Basin's very arid summer climate (O'Farrell et al. 1975). The disappearance of pocket mice forces nesting pairs to shift their forage attention almost exclusively to insects. Following the rules of Central Place Foraging Theory (Orians and Pearson 1979), owls must feed for small insect prey near the nest site where they eventually run into interference with nearby neighbors. Competition among pairs is not as evident early in the nesting season when rodent prey are abundant and pairs can forage at greater distances away from each other. This competition may also be exacerbated when available burrows greater than 110 m from existing nesting pairs is lacking.

Understanding this potential for high nest abandonment is important when using artificial nest boxes. We recommend that boxes be placed no closer than 110 m apart to help avoid competition stresses between neighboring pairs.

Brood Protection. The structure of artificial nest boxes may also affect nestling survival. While use of auxiliary burrows has been noted (Martin 1973, Henny and Blus 1981), we noticed this behavior was most apparent with owls using artificial nest boxes. We speculate that the standard artificial burrow configurations (30.5 × 30.5 cm; Collins and Landry 1977) we used can become too confining for large broods (i.e., >5) in advanced stages of development, forcing some nestlings to shift to auxiliary burrows. Broods in natural burrows expanded their nest chamber by digging the soft earthen walls. While we have no evidence that auxiliary burrow use decreases survivability of nestlings, we observed successful fledgings of more than seven members of a brood occurring only at natural burrows. We also observed that nestlings commonly widened the entrance to natural burrows allowing for several individuals to escape down the tunnel at once, whereas straight artificial tunnels generally only allow nestlings to escape single file. This could increase susceptibility to predation, especially by avian predators.

Based on our observations, we suggest that artificial nest boxes be constructed with walls at least 36 cm in length and width to accommodate large broods in advanced stages of development. Loose soil can be placed within the nest box along the sides to reduce the nest chamber size for attending females, but allow the nestlings easy means for expanding the chamber later. Three-wall designs would also allow nestlings to expand the nest chamber. Finally, a funnel design for the entrance may assist nestlings in quick escapes down the tunnel.

Prey Selection. An important component of the nesting habitat for Columbia Basin burrowing owls is a high percentage of bare ground. For example, Green and Anthony (1989) found that burrowing owls selected nest sites in areas where the average cover of bare ground was 55% and, conversely, the average cover of grass was only 28–36%, similar to findings ($\bar{x}$ = 35%) by MacCracken et al. (1985) for burrowing owls nesting in South Dakota. Dense grass may impede the movements (Tester and Marshall 1961, Rickard and Haverfield 1965, Gano and Rickard 1982) of important prey animals for local burrowing owls (Green et al. 1993). Also, higher populations of small mammals (Rogers and Hedlund 1980, Gano and Rickard 1982) and beetles (Rogers and Fitzner 1980) exist in shrub communities in the Columbia Basin with relatively low grass coverage. Vegetative and bare ground cover should be evaluated when selecting areas for establishing nesting pairs. Also, our observations of burrowing owls invading recently burned areas suggest that prescribed burning may be a useful tool for improving nesting habitat by removing dense grass cover.

Management Recommendations

With the rapid conversion of burrowing owl shrub-steppe nesting habitat to croplands in the Columbia Basin (Muckleston and Highsmith 1978), this species is becoming the focus of more management projects. Based on our earlier discussion, we provide a list of recommendations that consider several aspects of behavioral ecology including predator avoidance, intraspecific competition, brood protection, and prey selection. These recommendations are: (1) Provide elevated perches near potential nest burrows in grassland areas if the average vegetation height is 5–15 cm; (2) Provide fresh cattle dung near nesting areas if dung is not available and mammalian predators, especially badgers, occur in the area; (3) Place artificial nest boxes no closer together than 110 m; (4) Construct boxes with width and length dimensions of at least 36 cm and place soil around the inside wall; or construct boxes with only three walls. Make the tunnel entrance funnel-shaped; (5) Select sites for establishing or increasing nest sites that have approximately 55% (40–70%) bare ground and average shrub coverage of <15%; and (6) Conduct research on the utility of prescribed burning as a tool for enhancing owl nesting habitat.

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THE ONE-WAY DOOR TRAP: AN ALTERNATIVE TRAPPING TECHNIQUE FOR BURROWING OWLS

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ABSTRACT.—A population of 17 burrowing owls (*Speotyto cunicularia*) had to be removed from a construction site in Manteca, San Joaquin County, CA, in a two-week period. I used a trapping method that incorporated a one-way door surrounded by a wire mesh cage. One-way doors and cages were placed over burrow entrances so that owls were able to exit burrows yet remain within the cage (trap). Initial attempts using snare-type traps captured eight owls, yet proved to be time-consuming. The remaining nine owls were captured in half the time it took to capture the first eight owls. The ease of constructing and setting the trap, the potentially high capture rate, and the lack of trapping injuries, makes the one-way door trap an efficient alternative to other capture techniques.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *technique; trapping.*

La puerta de una sola direccion: Una tecnica alternativa para atrapar tecolotito enano

RESUMEN.—Una poblacion de 17 tecolotitos enanos (*Speotyto cunicularia*) se tuvieron que remover de un sitio de construccion en Manteca, condado San Joaquin, California, durante un periodo de 2 semanas. Use un metodo de atrapar que incorpora una puerta de una sola direccion rodeada de malla de alambre. Puertas de una sola direccion y jaulas se pusieron sobre las entradas de las madrigueras para que los tecolotes pudieran salir pero quedaban atrapados en la jaula. Atentados iniciales usando el metodo de trampas de lazo atraparon ocho tecolotes pero era demasiado tardado. Los otros nueve tecolotes se capturaron en la mitad del tiempo que se requirio para atrapar los primeros ocho tecolotes. La facilidad con la que se puede construir y plantear la tramp, la alta probabilidad de captura y el evitar lastimaduras hacen que la trampa de puerta de una sola direccion sea una alternativa eficaz a otras tecnicas de captura.

[Traducción de Filepe Chavez-Ramirez]

Methods for capturing burrowing owls (*Speotyto cunicularia*) include bal-chatri traps (Berger and Mueller 1959, Ward and Martin 1968, Smith and Walsh 1981, Yosef and Lohrer 1992), noose carpets (Bloom 1987), noose rods (Winchell and Turman 1992), mist nets (Ferguson and Jorgensen 1981), padded leg-hold traps (Haug and Oliphant 1990), and variations of Havahart or Tomahawk-type traps (Martin 1971, Ferguson and Jorgensen 1981, Plumpton and Lutz 1992). However, these traps can be time-consuming, labor intensive, and capable of capturing only one or two owls at a time. The objective of this study was to capture and relocate 17 burrowing owls, during the fledgling stage, from a construction site in Manteca, California, within a two-week period during summer 1992. Initial attempts to capture owls using one bal-chatri trap baited with a mouse and three noose carpet traps per burrow were successful, yet time-consuming. In addition, owls became trap-shy and eventually avoided the snare traps. For this reason, I developed and utilized a trapping technique incorporating a one-way door and cage to increase the capture rate.

MATERIALS AND METHODS

One-way doors were placed in the entrances of occupied burrows during mid-day after owls had descended into burrows to avoid high ambient temperatures. Each burrow entrance was then enclosed with a square 61cm × 61cm open-bottomed cage (Fig. 1). The one-way doors were constructed from 10.2 cm aluminum heating duct secured to a 10.2 cm metal collar. A clear, lightweight, Plexiglas door was attached to the ceiling collar with duct tape. The one-way door is designed to allow an owl to exit a burrow, but not reenter. Minor modifications were sometimes required for the installation of the one-way door. A cage was placed over each one-way door to capture exiting owls. The cage was anchored to the ground by tent stakes or bricks. Cages were constructed with poultry mesh and 2.54 cm PVC pipe. A trap door was cut into the top of the cage to permit removal of captured owls. Trapping occurred July 1992, between dusk and 0100 h and during early morning hours (i.e., 0500 to

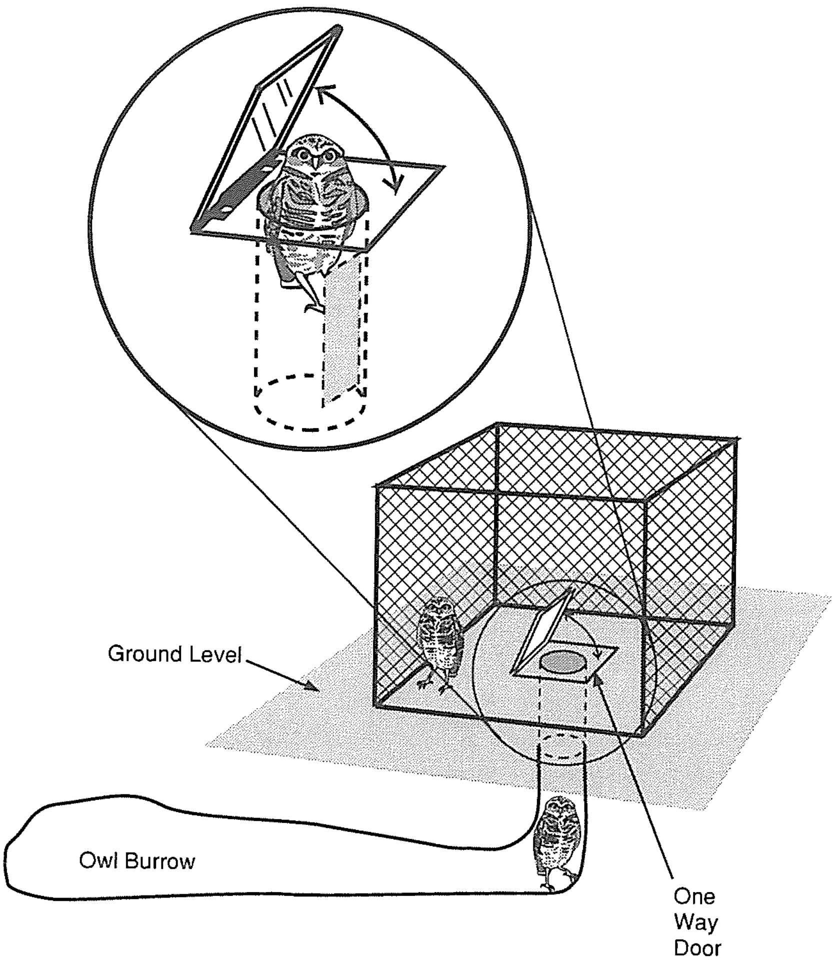

Figure 1. A one-way door trap for burrowing owls.

0900). Traps were monitored on an hourly basis. Captured owls were immediately removed and banded with U.S. Fish and Wildlife Service aluminum bands and plastic color leg bands.

Results and Discussion

Eight owls (six juveniles and two adults) were captured in 35 person-hours with an average of one bal-chatri and three noose carpet traps per burrow. This effort resulted in one owl capture per 4.3 hr, yet only half of the population had been captured. In contrast, the remaining nine owls (four adults and five juveniles) were captured in 19 person-hours using 4 one-way door traps (one trap per burrow). Six of the nine owls were captured in less than 2.5 hr, four of which were caught within a 15 min. time span, in three traps. Twice, two owls were captured in a single trap. Overall, the one-way door trapping effort resulted in one owl capture per 2.1 hours.

The one-way door trap captured nine owls twice as fast as the bal-chatri and noose carpet attempts. The one-way door trap captured adults and juveniles, whereas bal-chatri and noose carpets resulted in a predominance of juveniles. Multiple captures occurred twice, indicating a potential for capturing entire families in one attempt. All captured owls were unharmed and appeared calm while in the traps. Potential owl injuries can be further avoided by using an alternative material for the cage construction (e.g., plastic or nylon).

The ease of constructing and setting the trap, the minimal disturbance to the burrow, the lack of trap injuries and escapes, and the potentially quick rate of capture makes the one-way door trap an efficient alternative to mist nets, snare-type traps, padded leg-hold traps, and box traps.

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AGE IDENTIFICATION OF NESTLING BURROWING OWLS

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ABSTRACT.—Two rescued burrowing owl (*Speotyto cunicularia*) nestlings hatched and raised for release in a rehabilitation program were photographed during their first month of growth. The owls were weighed regularly and notes were taken of plumage changes and behavior. They were self-feeding and tearing up halved dead mice by 15 d.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *weights; nestling plumage; feeding ability.*

Identificacion de polluelos del tecolotito enano

RESUMEN.—Dos pollos rescatados de tecolotito enano (*Speotyto cunicularia*) que se empollaron y criaron para liberarlos en un programa de rehabilitacion se fotografiaron durante el primer mes de crecimiento. Los tecolotitos se pesaron regularmente y se tomaron apuntes de cambios en el plumaje y conducta. Los tecolotitos comian solos y destazaban ratones medio muertos a los 15 dias.

[Traducción de Filepe Chavez-Ramirez]

Burrowing owls (*Speotyto cunicularia*) in Santa Clara County, California were being routinely buried at construction sites. Nestling owls had little or no protection from earth-moving equipment, unless they were accidentally discovered. As director of a wildlife rehabilitation department for a local humane society in 1982, I started a burrowing owl rescue, relocation, and education program until better methods of burrowing owl preservation could be implemented. With the permission of the California State Department of Fish and Game and the U.S. Fish and Wildlife Law Enforcement officers, a team of volunteers and I removed only nests of owls that would otherwise be destroyed by construction equipment. This sometimes involved removal of eggs. After several years of raising nestlings and some hatchlings at our facility, we started receiving calls for advice on burrowing owl care from other rehabilitators in California. We found it difficult to estimate age and condition of the owlets over the telephone. Our initial literature searches had not indicated any useful information on the development of this species. Therefore, it became necessary to establish some comprehensive guidelines for aging burrowing owl young. My objective was not to compare weights and growth, but to have a general guideline of aging by plumage and weight. The following information is based on only two subjects and is intended as only a guideline. It is not a rigorous scientific study.

METHODS

In 1986 we removed three burrowing owl eggs from an active construction site in Santa Clara County, California. They were hatched on 3–5 June at the Predatory Bird Research facility in Santa Cruz, California. After the chicks were returned for raising, I selected the first and last birds hatched from the clutch to photograph and weigh. The three siblings were kept together. The nestlings were color-banded for identification and photographed at two d intervals or longer during the first month of growth. A box was laid on its side on a desk with a ruler propped upright inside. A Pentax K-1000 camera with a 50-mm lens was set on a tripod at approximately 1 m from the desk. Each two or three d the two owlets were removed from the nest area prior to their first morning feeding, placed next to the ruler, and photographed. With the exception of one 7-d period, the owls were weighed on a triple beam balance scale. I noted behavorial changes and development. The nest area was initially a large darkened tub with a K-101 K-pad at one end for an optional heat source. This pad is warmed by circulating warm water which produces a non-drying heat for brooding. The owls were fed commercially and home-raised dead mice, crickets, mealworms and beetles. Their food was not weighed. They were graduated to a large carrier with a burrow-type nest box and then at 30–32 d to a 3.05 m × 6.10 m flight aviary, complete with in-ground burrows. I worked alone and quietly when handling the owls. I sometimes mimiced their vocalization, which was a raspy "pssssst, pssssst." Because these owls were in rehabilitation and for release there was as little human contact as possible. It became increasingly difficult to persuade them to stand in position in the photo area and photography was impossible after 30–32 d of age.

Table 1. Plumage changes of two nestling burrowing owls observed in captivity.

DAYS OF AGE	PLUMAGE CHARACTERISTICS
8	Wings, head, back and nape pinned. Head is darkening with pin feathers. Second down blooming* on tibiotarsus and breast.
11	Back feathers emerging.
13	Primaries pinned 20 mm, back feathers emerging at nape and shoulders, upper breast covered with second down, tarsus pinned. Throat pinned. First down visible and sparse.
15	Body covered with second down. Legs feathering. Head feathering. First down still visible on head. Second down on wing coverts.
17	Primaries blooming and visible, back feathering well, some throat feathering with dark brown edge.
19	Primaries blooming and visible, back feathering well, some throat feathering with dark brown edge.
22	Throat is white with dark edge.
24	Tail pinned 12.5 mm.
26	Legs well feathered, small trace of white down on crown.
28	Little change.
30	Tail emerging.
32	Juvenile breast feathers emerging, tail 25 mm long. First down barely visible.

[a] The term "blooming" is used to describe the opening of the feather from the shaft.

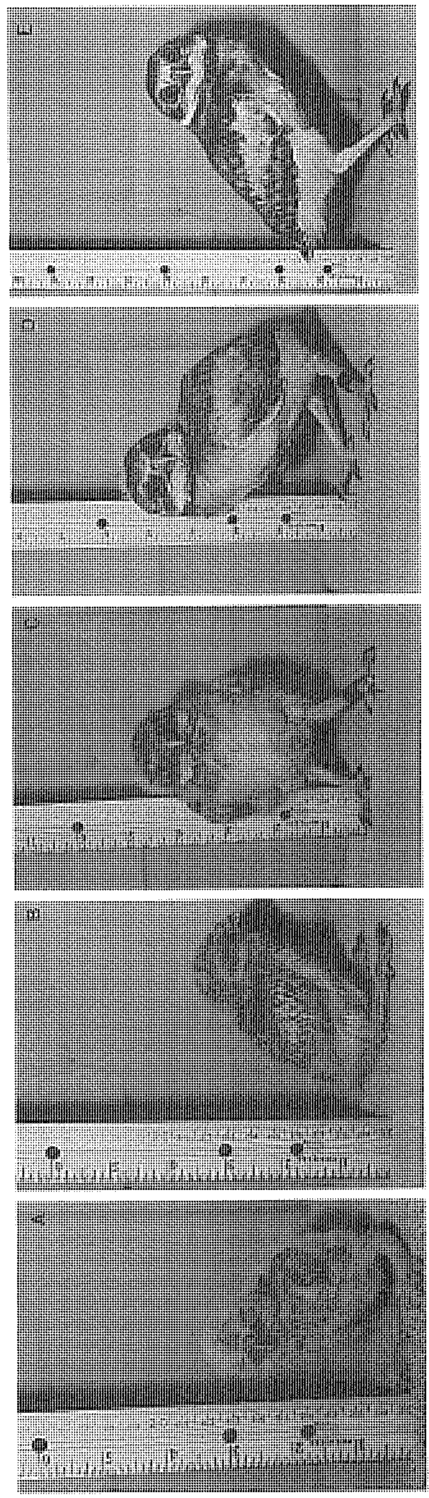

Figure 1. Burrowing owls at selective ages. A. Eight days. B. Eleven days. C. Fifteen days. D. Twenty-one days. E. Thirty-two days.

RESULTS AND DISCUSSION

The burrowing owls went through two down plumage stages. The first down, at hatch, was white; the second down, which emerged at about 8 d of age (on the breast, flank, and wing covert area) was tan. (Table 1 and Figure 1). I did not record observations on these two owls prior to eight d of age. I do, however, have notes and weights on earlier ages from more recently-hatched burrowing owls which are not included it this paper. The older owl weighed more than the younger owl when photographed at the same age (Table 2). Weights might be affected during the self-feeding period. The primary purpose of these owls was rehabilitation, so regular routines were upset as little as possible. I did not determine light availability during the photographing period; however, hand-raised birds are allowed normal daylight hours in a nonheated room, with open windows until they are

Table 2. Weights of two captive-raised burrowing owl nestlings. Owl A was hatched 3 June 1986 at 0500 H; Owl B on 5 June 1986 at 2315 H.

DATE	BIRD	WEIGHT (g)	DAYS OF AGE
13 June	A	63.0	10
	B	45.5	8
16 June	A	123.0	13
	B	81.5	11
18 June	A	122.0	15
	B	97.0	13
20 June	B	108.0	15
24 June	A	142.0	21
	B	125.0	19
27 June	A	161.0	24
	B	140.0	22
5 July	A	177.0	32
	B	143.0	30
9 July	A	151.0	36
	B	143.0	34

transferred into an outside flight aviary. I noted that on d 11 mouse pieces were being picked up (Table 3). I did not distinguish in my notes which of the owls had consumed the mouse bits. It has been my practice to feed nestling burrowing owls from below, rather than from above, and drop mouse bits or insects in front of them in order to draw their attention to the food, not the feeder, and to encourage self-feeding. I have observed younger burrowing owls (prior to eyes opening) walking about the nest tub on their ankles at feeding time with their faces to the floor, turning their heads from side to side in a sweeping motion, calling and biting at anything.

Table 3. Behavior and development of captive burrowing owls (based on general notes taken of three nestling owls).

DAYS OF AGE	BEHAVIOR AND DEVELOPMENT
8	Walks and sits on ankles, can stand.
11	Eyes opening, can stand, will pick up mouse bits from floor of nest area.
13	Eyes open, standing well, some defensive posturing.
15	Self-feeding, tearing up halved mice.
17	Doing defensive posturing in my presence.
19	Independent and self-feeding.
21	Tearing up whole mice.
26	Alert, independent, objects to handling.
32	Uncooperative, wants no part of humans.

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OBSERVATIONS, RESIGHTINGS, AND ENCOUNTERS OF REHABILITATED, ORPHANED, AND RELOCATED BURROWING OWLS

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ABSTRACT.—This paper describes data on 46 burrowing owls (*Speotyto cunicularia*), of which 40 were part of an ongoing rehabilitation and release program at the University of California, Davis, (UCD) and the others the subject of two unrelated relocation efforts between 1981 and 1991. Of the 40 owls which came to the UCD Raptor Center as the result of illness, injury, or being orphaned, 9 died or were euthanized; 9 were non-releasable and transferred to other institutions for breeding and/or research; 6 were released unbanded; and 16 were banded and released in occupied or unoccupied burrows within an established colony on the UCD campus. Nine orphaned HY owls were fostered, five of which (55%) were encountered or resighted. Two were encountered 3 and 5 days postrelease after colliding with large windows near the release site. One owl encountered 12 d postrelease was retrapped at the release site. Two other fostered owls were resighted up to 28 days and 34 d postrelease, respectively. These two used both the original release burrow and satellite burrows within 27 meters. Of 5 adult rehabilitated owls released, one was found 80 d postrelease after colliding with a vehicle (CV) approximately 183 m from the release site. Two adult owls were trapped and then relocated 0.8 km on the campus of the University of California, Davis, in December 1981; they were encountered 426 d (dead due to CV) and 1,310 d (retrapped near the release site) respectively. In a separate relocation project using one-way burrow exits on the Consumnes River College campus, all owls relocated themselves to artificial burrows placed 45 m away between November 1988 and January 1989. In another effort, in June 1991, six burrowing owls were relocated from a development site in Sacramento; three owls relocated 24 km from the site and three relocated 48.3 km. Of the 6 relocated owls, 5 were observed between 10 and 49 d postrelease. One adult female observed 10 d at the relocation site returned 24 km to her original territory, arriving 32 d postrelease. These data suggest that although some burrowing owls develop a strong fidelity to a relocation site, others tend to disperse after a period of adjustment at the site of release.

KEY WORDS: *burrowing owl;* Speotyto cunnicularia; *relocation; rehabilitation; fostering; resighting; encounter; mortality; California.*

Observaciones, reobservaciones, y encuentros de tecolotitos enanos rehabilitados, huérfanos, y relocalizados

RESUMEN.—Este escrito describe datos sobre 46 tecolotitos enanos (*Speotyto cunicularia*) de los cuales 40 fueron parte de un programa de rehabilitacion y liberacion de la University of California, Davis, (UCD). Los otros eran parte de dos esfuerzos no relacionados de relocalización entre 1981 y 1991. De los 40 tecolotes que llegaron a UCD Raptor Center como resultado de enfermedad, lastimadura, or por ser huérfanos, 9 murieron; 9 no se podian liberar y se transfirieron a otras instituciones para su reproduccion y/o para investigacion; 6 se liberaron sin anillar; y 16 se anillaron y se liberaron en madrigueras ocupadas o no ocupadas en colonias en el campus de UCD. Nueve tecolotitos huerfanos del año se criaron, de los cuales cinco se encontraron o se reobservaron Dos se encontraron 3 y 5 días después de haberse liberado cuando chocaron con grandes ventanas cerca del sitio de liberacion Un tecolote encontrado 12 días después de liberarse se atrapo en el sitio de liberacion. Otros dos tecolotitos criados se reobservaron hasta 28 y 34 días después de liberarse. Estos dos utilizaron la madriguera de liberacion y madrigueras satélites hasta 27 metros. De 5 tecolotes adultos rehabilitados y liberados, uno se encontro 80 días después de liberarse cuando choco con un vehículo (cv) aproximadamente a 183 metros del sitio de liberacion. Dos tecolotes adultos se atraparon y se relocalizaron 08 km en el campus de la

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University of California, Davis, en diciembre 1981; se encontraron 426 dilas después (muertos debido a cv)y 1,310 días (reatrapado cerca del sitio de liberacion), respectivamente. En un poyecto diferente de relocalizacion utilizando salidas de-una-sola-direccion en el campus de Consumnes River College, todos los tecolotes se relocalizarón independientemente a madrigueras artificiales puestas a 45 metros entre noviembre 1988 y enero 1989. En otro esfuerzo, en junio 1991, seis tecolotitos enanos se relocalizaron de un sitio en desarrollo en Sacramento; 3 tecolotes se relocalizarín 24 km del sitio y tres se relocalizarón 483 km. De los 6 tecolotes relocalizados 5 se observaron entre 10 y 49 días después de liberarse. Un hembra adulto observada 10 días en el sitio de relocalización regreso 24 km a su territorio original arribando 32 días después de liberarse. Estos datos sugieren que aunque algunos tecolotitos enanos desarrollan gran fidelidad a su sitio de relocalización, otros tienden a dispersarse después de un periodo de ajuste en el sitio de liberacion.

[Traducción de Felipe Chavez-Ramirez]

Burrowing owls (*Speotyto cunicularia*) were rehabilitated and released within an established colony on the University of California, Davis (UCD) campus in order to augment a declining population and to observe and document postrelease behavior, survival, and mortality (Johnson and Schulz 1985). The burrowing owls on the UCD campus provided a valuable resource for both undergraduate and graduate studies and allowed the public an opportunity to view and further appreciate this unique and relatively visible owl. To mitigate the effects of the campus maintenance and development, the UCD Raptor Center, School of Veterinary Medicine, worked closely with the campus grounds division to manage the available nesting and foraging habitat on behalf of the burrowing owls. Occupied burrows were located and identified. Burrows were considered occupied if they had adult owls using them and/or they had fresh pellets, fecal droppings, and feathers at or near their entrance. Soil in the PVC pipe brought in by the owls' feet was another indication of activity in the burrow. The grass was periodically mowed to a height of approximately 15.2–22.9 mm, artificial perches were erected, and six artificial burrows were constructed and placed in one of the burrowing owl habitats (Collins and Landry 1977) and (Olenick 1987). The UCD Raptor Center staff also worked closely with rodent control personnel and participated in annual control meetings by giving talks on how to identify occupied burrows to assure that owls were not indiscriminately poisoned or gassed and that rodent control did not take place in fields inhabited by burrowing owls. In addition, UCD Raptor Center staff, local conservation groups, and concerned citizens convinced campus officials to set aside the nesting areas and place informative signs and fences on the periphery of burrowing owl habitat. A committee was formed to advise the campus on natural resources and open spaces. Despite these efforts, the burrowing owl disappeared from its former nesting areas on the UCD campus by 1991 (Johnson 1992). This paper provides information on the fates of 22 burrowing owls released between 1981 and 1991.

STUDY AREA AND METHODS

The UCD campus is located in the Sacramento valley 24 km west of Sacramento in Yolo County, California. The burrowing owl habitat was in flat, open, ruderal fields that had populations of the California ground squirrel (*Spermophilus beecheyi*). Injured and orphaned owls were initially treated at the UCD Veterinary Medical Teaching Hospital when necessary and then transferred to the UCD Raptor Center (California Raptor Center) for observation and rehabilitation. Hatching year (HY) birds without injuries were evaluated and released (fostered) on campus as soon as possible into burrows occupied by wild pairs with young of similar ages (Olendorff et al. 1980).

Adult injured owls were initially rehabilitated using physical therapy and then placed in flight cages until they were capable of strong, even flight ability (Schulz and Horowitz 1982; Horowitz, Schulz, and Fowler 1983). Sixteen out of 22 rehabilitated owls released were banded with U.S. Fish and Wildlife Service bands. Release areas were monitored using 7 × 42 binoculars at least four mornings a week until the released birds could no longer be located.

Three relocation projects are of special interest. The first occurred in 1981 when two adult birds were trapped with monofilament noose (bal chatri) traps at burrow entrances and relocated approximately 0.8 km from one area of the campus to another.

Another relocation project at Consumnes River College in southern Sacramento County was undertaken in 1989. The purpose of the relocation was to prevent accidental destruction of burrowing owls living in burrows on the site of an impending new road construction project. Six artificial burrows were placed 45.7 m south of the construction area on a north and west facing berm that surrounded a football field. The burrows were constructed with 152.4 mm diameter corrugated PVC pipe extending 120 cm into the side of the berm and turning 90° for another 120 cm into a 34.8 cm by 47.4 cm rectangular nest chamber constructed of cement. The base of the chamber was open and had 30 cm of rock and sand base for drainage. The area was surveyed on six different days between 6 November 1988 and 21 January 1989. In January 1989, five, one-way exits (Johnson 1992) were placed in the entrance to active burrows at the construction site. The one-way exits remained in place for one week to prevent reentry into burrows by the owls. At the end of the week burrows were filled with dirt. This method has the advantage of not requiring trapping or hands-on manipulation of the owls.

In a third project in 1991, six burrowing owls were trapped with noose traps and relocated to mitigate for future development in their habitat. Their habitat (in ruderal fields) was in a populated urban area of Sacramento, California. Three of the birds were relocated at artificial burrows on the UCD campus 24 km west of the original site, and the other three were relocated approximately 48.3 km west of the original site to a nonnative grass field with artificial burrows approximately 9.6 km north of Winters, Solano County, California. One dead mouse per bird and approximately 200 live crickets were placed in each burrow entrance. Monitoring alternated each day at sunrise and sunset, respectively.

Results and Discussion

A total of 40 sick, injured, or orphaned burrowing owls were treated by the UCD Raptor Center between 1980 and 1988. Twenty-two (55%) were eventually released. Of the 17 HY burrowing owls, 43% were received in June and 19% in July. Six (28%) of the 23 adult burrowing owls were received between June and September. Burrowing owls were brought to the UCD Raptor Center for a variety of reasons, the most noteworthy (25%) being collisions with vehicles (CV). Four owls (9%) collided with large windows or buildings. Fourteen (32%) had either wing fractures or coracoid fractures; 4 of these (29%) were eventually released. Nine (22.5%) owls died or were euthanized, and 9 were nonreleasable and transferred to other institutions for breeding and research projects.

Five of the nine HY owls fostered into occupied nests were encountered or resighted. Two of these were encountered three and five days postrelease, respectively, due to collisions with large windows; one was encountered 12 days postrelease and was retrapped (Johnson pers. comm.) at the release site; and the remaining two were resighted up to 28 and 34 days, respectively. Fostered owls appeared to interact normally with nonsibling juveniles and were fed by adults. They used satellite burrows within 27 m of the release site burrow. The method of fostering HY owls into active burrows with similar age birds allowed the young, inexperienced owls time to socialize with nonsibling conspecifics and sharpen their prey-catching skills while being fed by adult owls (Olendorff et al. 1980). However, more data are needed to evaluate the success of this technique. It is not known what caused the owls to fly into windows, although stray dogs were frequently seen chasing owls in the fields on campus. Dogs have also been observed chasing ground squirrels and digging at burrow entrances. Cats in the owl habitat could also have had a serious impact on the population.

Only one adult of seven injured and rehabilitated adult owls was later encountered. This individual had a coracoid fracture on 29 October 1985 and released 17 January 1986 on the UCD campus. It was encountered approximately 183 m from the release site after 80 d, dead due to CV.

The two adult owls trapped on the UCD campus in December 1981 were relocated 0.8 km to another site on campus. The first encounter was 28 November 1983, 426 d postrelease. The owl was dead due to CV approximately 0.8 km from the relocation site. The second relocated owl was retrapped near the release site in good condition on 6 June 1985, 1,310 d postrelease (Johnson pers. comm.).

From 1980 to 1990, 22 burrowing owl deaths were documented on the UCD campus. Ten of these (45%) were CVs; five (22.7%) were killed by feral (domestic) cats; four (18%) collided with windows; and three (13.6%) died of unknown causes. Therefore, 20 owls were documented to have been hit by vehicles (half survived as noted earlier). Their low, undulating flight behavior may be an important factor in their susceptibility to collisions with moving vehicles.

In the passive relocation effort at Consumnes River College, all six owls relocated themselves, and at least two were observed at the entrance to the artificial burrows within 1 wk. More owls were observed on the stadium berm during subsequent surveys. No owls were seen at the construction site after their burrows were destroyed. Although owls moved from the construction area into artificial burrows 45.7 m away, there is no certainty that the individuals observed were the same birds because they were not banded. However, Trulio (pers. comm.) observed that by using the technique described above, banded owls successfully relocated themselves into nearby artificial burrows.

In the third relocation effort involving six burrowing owls, the three owls relocated from Sacramento to the Davis campus were a mated pair with one juvenile approximately 6–7 wk old. The female remained at the release site up to 10 d and was later observed at her original territory after 32 d. She was retrapped and relocated but did not remain more than a day. The juvenile was observed for at least 14 d and was not seen after that. The adult male was observed 49 d postrelease near the relocation site. The other three nonmated owls relocated approximately 48.3 km west of the original site and 9.6 km north of Winters, California, were placed into separate artificial burrows. Two of the owls were resighted at the relocation burrows up to 24 and 42 d, respectively. The third owl was not observed after release.

These data suggest that some relocated owls may remain at release sites while others tend to disperse and even return to their original territory after a period of adjustment. Although relocation efforts may temporarily remove individual owls from potential destruction, more data are needed on long-term effectiveness. This method of mitigation should be carefully considered and only used as a last resort.

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BURROWING OWL SITE TENACITY ASSOCIATED WITH RELOCATION EFFORTS

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ABSTRACT.—A pair of burrowing owls (*Speotyto cunicularia*) exhibited strong site tenacity during an effort to relocate them from a development site in San Joaquin County, California during the winter and fall of 1992. This case prompted an inquiry among other biologists working with burrowing owls to see if they had had similar experiences. Their responses allowed me to present additional examples of site tenacity in efforts to relocate burrowing owls along the Pacific coast. Potential benefits of site tenacity and considerations for relocation success are also discussed.

KEY WORDS: Speotyto cunicularia; *burrowing owl; California; relocation; Washington; British Columbia.*

Tenacidad de sitio asociada con esfuerzos de relocalizacion de tecolotitios enanos.

RESUMEN.—Un par de tecolotitos enanos (*Speotyto cunicularia*) exhibieron fuerte tenacidad de sitio durante esfuerzos para relocalizarlos de un sitio en desarrollo en el condado San Joaquin, California durante invierno y otoño de 1992. Este caso causo que averiguara entre otros biologos trabajando con el tecolotito enano para determinar si habian tenido experiencias similares. Sus respuestas me ayudaron a presentar ejemplos adicionales de tenacidad de sitios observados en esfuerzos de relocalizacion de tecolotito enano a lo largo de la costa del Pacifico. Beneficios potenciales de tenacidad de sitio y consideraciones para el exito en relocalizacion tambien se discuten.

[Traducción de Filepe Chavez-Ramirez]

There are at least three reasons to relocate burrowing owls: to (1) protect them from risk when their habitat is being altered or destroyed; (2) rebuild depleted burrowing owl populations by translocation from healthy populations; and (3) protect endangered prey species.

Two relocation methods have been used with considerable variation of technique in removing burrowing owls from a particular location. The first is removing the burrow systems by digging out or closing burrows, leaving the owls to independently relocate. This method is usually applied when it has been found that there is nearby or adjacent habitat available. The second is trapping and relocating the owls directly to a new site which is considered to be suitable habitat some distance from the original site.

Along the Pacific states, particularly in the San Francisco Bay area, there have been a number of projects involved with moving burrowing owls, resulting in varying degrees of success (Dyer 1991, Harris and Feeney 1989, H.T. Harvey & Assoc. 1993). Occasionally, burrowing owls can show considerable original site tenacity causing complications and negative results. Burrowing owls at a development site in San Joaquin County, CA led me to investigate the topic of site tenacity and compile information from several sources. Source material for additional information came from biologists and consulting firms willing to share their experiences. Although information from some of the cases is anecdotal, and some specific details have been lost in time, the fundamental lessons learned can assist those who find it necessary to move and/or protect burrowing owls.

In December of 1991, I was asked to move a pair of burrowing owls from a cul-de-sac of lots with partial improvements already installed so that the builder could finish constructing homes during the spring of 1992. The site is in the city of Tracy in San Joaquin Valley, California. Several open fields were available to these owls within a few hundred meters of their burrow. Some of these held owls, and most had ground squirrels and unoccupied burrows. After consulting with the California Department of Fish and Game, it was decided to close out the burrows of the resident owls on the construction site, and let the owls relocate themselves. Evening observations showed that the owls were compatible with and foraged with four pairs of owls nearby.

METHODS

The first burrow closure effort was initiated in January, 1992 by flushing the birds on several occasions to confirm that they were familiar with available nearby unoccupied burrows. The owls flew directly to burrows either in the adjacent field or to burrows along a drainage canal within 100 m. The owls' main burrow and satellite burrows on the development site were then dug out and filled in. Burrows were closed until it was confirmed that the burrowing owls had chosen a home burrow off the site. I made twenty-nine visits (involving about 90 hr) to the site between 21 Jan. 1992–22 Mar. 1992. One visit was made to the site in April, 1992 and then twice a month through May, June, July, and August 1992 to monitor the activity and location of burrowing owls on the site and in adjacent fields during the breeding season. In addition, local homeowners and a schoolteacher, who wanted to protect the owls, monitored the owls almost daily.

The second burrow closure effort at the same site began in early September 1992 and continued until late November 1992. The second effort received continued support from local citizens. Four artificial burrow systems were constructed beginning at 100 meters from the cul-de-sac site on the bank of the drainage canal, each system separated by 35 m. The burrow cavities were made of heavy plastic water valve boxes (25.4-cm × 40.6-cm at the top; 30.5-cm deep) with removable lids. Two holes were cut in the end for the placement of four-inch plastic corrugated tubing, and a portion of one side of the box was removed so the burrow cavity would have at least one dirt wall. The boxes were buried <1m underground. Light-colored sand was placed at the entrance of the burrows to facilitate easy reading of tracks into the burrows. Burrowing owls from the cul-de-sac site were flushed from the site beginning 18 Sept. 1992. Burrows at the cul-de-sac were filled in after flushing the birds from the site. Closing burrows and flushing the birds continued until the owls were no longer observed at the cul-de-sac development site. Thirty visits (84 hr) were made to the site from 3 Sept. 1992–29 Nov. 1992.

RESULTS

The first effort (January–March 1992) to remove the burrowing owls from the cul-de-sac site resulted in having to close burrows thirteen times at the cul-de-sac before the owls chose another burrow on the berm of the nearby canal, 100 meters away. They stayed off the cul-de-sac site for at least two weeks in March. In late April 1992, it was reported that one of the pair which had moved to the canal had been shot with a pellet gun (Linda Smith pers. comm.) and presumably its mate returned to the cul-de-sac where ground squirrels (*Spermophilus beecheyi*) reopened some of the closed burrows. At about the same time, four additional owls (two pairs) moved to the cul-de-sac area. There were then five burrowing owls residing on the development site, and it was their breeding season. The property owners agreed to let the birds use the property for the 1992 breeding season, but requested that we renew efforts to remove them from the site in September of 1992. Visits through the summer revealed that the two pairs of owls had young, and that a single bird remained on the site, always seen alone at the same burrow. On 3 Sept. 1992 the two burrowing owl families were absent from the development site; however, the single bird was present at its burrow on the cul-de-sac. On 6 Sept. 1992 the burrow occupied by the single bird hosted two adult birds, suggesting that the single bird had acquired a mate. The birds were, however, unbanded, so this late summer pairing could not be confirmed.

Flushing the birds from the site and filling in burrows began again on 18 Sept. 1992 after owl tracks had been seen at all of the new artificial burrow entrances. Most observations in late September and October revealed a pair of owls at burrows on the cul-de-sac which were either opened by ground squirrels or the owls themselves. One owl was observed digging on two occasions at locations where burrows had been filled. I closed any burrows I found opened by animals on every visit. On two visits the owls were found huddled under vegetation near their closed burrow with no other burrows available. A shooting incident on the cul-de-sac resulted in the killing of two rock doves (*Columba livia*) with a pellet gun, and possibly caused the injured right leg on one of the owls observed at the same time (13 Oct. 1992). The incident appeared not to deter the owls; they remained at the cul-de-sac. A burrow was opened for the injured bird which the pair used; however, trapping efforts to catch and rehabilitate the injured bird failed. The burrow was closed again on 21 Oct. 1992. The birds were last seen at the cul-de-sac on 6 Nov. 1992, and missing on 8 Nov. 1992. Neither the injured bird nor any additional birds could be located at nearby fields or other local habitat during subsequent visits through November 1992.

Two pairs of burrowing owls successfully fledged young at the canal where artificial burrows were placed during both the 1993 and 1994 breeding season (Larry Vasco pers. comm.) indicating that the artificial habitat attracted some of the local burrowing owls even though the target owls initially resisted moving to the area.

OTHER CASE HISTORIES

The site tenacity exhibited by burrowing owls in San Joaquin County led me to inquire among colleagues to see if they had had similar results with burrow closure or relocation efforts. In addition to a second experience I had (Case 2, below), I received three accounts of birds remaining at sites after burrow closure, nine accounts of banded owls that returned to original sites after relocation, and one relocation effort (Case 8) that resulted in no return. Details of each case varied considerably, with relocation distances from 1–150 miles and original sites located from San Diego, California to central Washington. Another factor that varied considerably was the time of year. Relocation efforts from January through December had at least some burrowing owls resisting a new location by staying at or returning to the original burrow sites. Brief accounts of these cases follow.

BURROW CLOSURE

Case 1. Lake Elizabeth, Fremont, Alameda Co., CA.

REASON	NO. OWLS	SEASON	NEAREST HABITAT
Vandalism	2	Breeding	Adjacent

Vandals destroyed eggs in a shallow nest and blocked burrow entrance. Burrow was closed for about a week. Owls were not banded and were not detected when burrow was opened, but one week after burrow was opened a pair of owls was found at the burrow. Only one pair was known in the vicinity, and the owls at reopened burrow were presumed to be the same that lost their nest.

Case 2. Alameda, Alameda Co., CA.

REASON	NO. OWLS	SEASON	NEAREST HABITAT
Development	2	Fall/Winter	Adjacent

In November 1986 the location of a burrow used by a pair of unbanded owls was leveled, graded and completely cleared of vegetation. A pair of owls, presumed to be the same birds that lost their burrow, was seen on several occasions near the destroyed burrow site. They were last seen on 5 Jan. 1987 using a pile of discarded construction materials about 100 m from the burrow site for cover. The following day a 10-ft-wide ditch was created at the location of the debris pile; the owls could not be found.

Case 3. Cedar Blvd. and Balentine Dr., Newark, Alameda Co., CA.

REASON	NO. OWLS	SEASON	NEAREST HABITAT
Development	4	Fall	<760 m away

Owls flushed from site (20 Sept. 1990) and nest burrows were excavated prior to disking the same day. One pair used depressions in ground for cover at the site after the burrow was destroyed. On 7 Oct. 1991 (last visit) one owl was seen at site of destroyed burrow.

Case 4. Mission College, Santa Clara, Santa Clara, CA.

REASON	NO. OWLS	SEASON	NEAREST HABITAT
Development	12	Summer	<150 m away

Burrows excavated and closed 10 Aug. (year not provided). One pair remained near destroyed burrow at the construction site until the last visit on 21 Aug. of the same year. Another pair moved to another burrow about 500 ft away. A single adult and seven juveniles were not observed again.

RELOCATION

Case 1. Cushing Parkway and Northport Drive, Fremont, Alameda Co., CA.

REASON	NO. OWLS	SEASON	DISTANCE RELOCATED
Unknown	3	Fall	<19 km

Kept in aviary at new site from 30 Oct.–7 Nov. 1989 when they were released. On 14 Nov. only one owl remained at relocation site and it stayed until at least 22 Nov. 1989.

Case 2. Mission College, Santa Clara, Santa Clara Co., CA.

REASON	NO. OWLS	SEASON	DISTANCE RELOCATED
Development	10	Late winter	Approximately 30 km

Kept in aviary at new site from 3–4 Mar.–15–16 Mar. 1990, when they were released. Found missing on 6 Apr. and 24 May 1990. Three pairs returned to original site; 6–8 June 1990, 19 July 1990, 7 Aug. 1992. One male owl, which was relocated to new site remained at that site until at least August of 1992.

Case 3. San Jose, Santa Clara Co., CA.

Reason	No. Owls	Season	Distance Relocated
Unknown	1	Fall	Approximately 40 km

Taken to relocation site 30 Apr. 1986 and found back at the original site 27 May 1986. Bird was re-trapped in summer of 1987 and released in Cholame, San Luis Obispo Co., CA about 200 mi south of original site. It was not seen again.

Case 4. South San Jose, Santa Clara Co., CA.

Reason	No. Owls	Season	Distance Relocated
Development	2	Spring	Approximately 32 km and 64 km

Taken to relocation site 30 Apr. 1986. Found at original site on 3 June 1986 at a burrow near original burrow with 5 eggs. Birds recaptured and re-released 40 mi south of original site. They were not known to return.

Case 5. Mountain View, Santa Clara Co., CA.

Reason	No. Owls	Season	Distance Relocated
Rescue	1	Fall	45 km

Rescued from stairwell and released 21 Nov. 1985. Bird found back near original location; date not provided.

Case 6. Coronado Island Naval Air Station, San Diego, San Diego Co., CA.

Reason	No. Owls	Season	Distance Relocated
Predation	2	Breeding	48 km

Burrowing owls taking least tern (*Sterna antillarum browni*) young; relocated owls to the north, and they were back at the original site the same day.

Case 7. Coronado Island Naval Air Station, San Diego, San Diego Co., CA.

Reason	No. Owls	Season	Distance Relocated
Predation	2	Breeding	48 km

Burrowing owls taking least tern young; relocated owls to the east, and they were found at the original site when biologist returned on the same day.

Case 8. Coronado Island Naval Air Station, San Diego, San Diego Co., CA.

Reason	No. Owls	Season	Distance Relocated
Predation	4	Breeding	>144 km

Burrowing owls taking least tern young; relocated owls to the east at Anza Borrego State Park, San Diego Co., CA and Salton Sea National Wildlife Refuge, Imperial Co., CA. Relocation site now provided a 5000 ft mountain range barrier to original site. Owls did not return to original site.

Case 9. Bay Farm Island, Alameda, Alameda Co., CA.

Reason	No. Owls	Season	Distance Relocated
Development	4	Fall	<1.6 km

Two wild and two rehabilitated burrowing owls were banded and kept in an aviary for 5 d at new location (November 1986). One bird was seen at the relocation site sporadically for the first two weeks after release, then disappeared. Another owl was found nesting at original site in April 1987 with an unbanded mate. The two rehabilitated owls stayed at the relocation site and brought unbanded mates to the artificial burrows by the end of December 1986.

Case 10. Moses Lake Area, Grant Co., WA.

Reason	No. Owls	Season	Distance Relocated
Translocation	55	Summer	Approximately 240 km

Ten adults and 45 hatchlings relocated to Osoyoos Lake, British Columbia (BC). Most adults dispersed from the release site by the end of the first week, July 1985. Thirty-eight juvenile owls fledged and all dispersed September 1985. In March of 1987 one owl released in BC was recovered at original trapping site in Washington. A second banded bird at original site was presumed to be a returned transplanted bird. Other adults have since returned to Washington. Transplanted hatchlings had not been observed returning to Washington as of October 1992.

Discussion

Contributors to the above cases offered suggestions for the burrowing owls' resistance to leaving an area or to their returning to an original site location: (1) there may be a bond to an active nest and/or home territory; (2) breeding success or simply survival at the original site for one or more years is thought to intensify the territorial bond; (3) attachment to a mate and/or colony social structure may be a consideration for territorial bonding; (4) low or unfamiliar prey base at new location may cause site rejection; (5) the presence of predators at the new location can cause direct risk to the owls or competition for prey and abandonment; (6) unfamiliar disturbance(s) can intimidate owls at a new location; and (7) there may be potential for errors at the new location in artificial habitat strategies, such as the design and/or placement of artificial burrows.

The tendancy to reuse an established breeding site has been recorded for a wide variety of avian species (McNicholl 1975, Shields 1984, Atwood and Massey 1988, Dobkin et al. 1986). Numerous studies have shown that reproductive success influences the continued use of avian breeding sites (Freer 1979; Harvey et al. 1979; Burger 1982; Newton and Marquiss 1982; Oring and Lank 1982; Redmond and Jenni 1982; Calder et al. 1983; Dow and Fredga 1983; Burger 1984; Shields 1984). It has also been shown that familiarity with habitat surroundings and neighboring individuals reduces risks with at least larids (McNicholl 1975).

Predation of burrowing owls at new sites has been documented. A burrowing owl relocation project in Minnesota resulted in a great horned owl (*Bubo virginianus*) causing the loss of all relocated burrowing owls (Dyer 1987). Great horned owls have also taken young peregrine falcons (*Falco peregrinus*) reintroduced to natural cliffs along the east coast of the United States (Newton 1979).

Tengmalm's owls (*Aegolius funereus*) avoided nest boxes or natural holes in which they suffered predation the previous year, suggesting that predation can cause nest site abandonment for this owl (Sonerud 1985).

The need for additional information to help determine the best strategies for successful burrow closure and relocation projects points to the importance of careful long term monitoring and sharing of results.

There will be more development, and biologists will continue to get calls to move burrowing owls for one reason or another. The above-mentioned references suggest that site tenacity is very likely a mechanism designed to assist birds in survival and breeding success. Coaxing burrowing owls to overcome site tenacity during burrow closure and relocation projects will have a greater chance of success if we have a thorough understanding of the ecological details of the original and relocation sites and the life histories of the owls involved. With this information in hand, we can design more successful relocation schemes.

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RELOCATION OF BURROWING OWLS DURING COURTSHIP PERIOD

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ABSTRACT.—Five pairs of burrowing owls (*Speotyto cunicularia*) were relocated from a site in Santa Clara, California, to two sites located approximately 31 km to the south, in March 1990. Ten owls were trapped in mid-February and released from hacking aviaries in mid-March three to four weeks after capture. We supplemented food from the date of capture, and the amount of food was gradually diminished to zero over time. We monitored local movements of the ten owls. Two pairs of owls bred successfully at each of the two relocation sites (STL and ARC). One of these produced six nestlings, at least two of which survived to fledging. The second pair produced eggs and young, but the nest failed due to predation. Two other pairs attempted breeding (i.e., nest construction), but the male of one pair was killed by a predator prior to the egg-laying stage and the second pair left the site. Three female owls, all of which had experienced a failed nesting attempt, left the relocation sites and returned to the capture site. Six owls remained at the STL site in 1991, and two owls were still present in 1992. A pair of owls attempted to nest at the ARC site in 1991, and at least one owl has been observed at the site through 1994. Although the relocation sites were to be managed in the long term for burrowing owls, these management plans were not followed, and owls generally dispersed by the end of 1991. This study indicates that burrowing owls may be successfully relocated if birds are moved at the beginning of the breeding season.

KEY WORDS: *burrowing owl*; Speotyto cunicularia; *relocation*; *courtship period*; *hacking*; *California.*

Relocalizacion de tecolotito enano durante el periodo de cortejo

RESUMEN.—Cinco pares de tecolotito enano (*Speotyto cunicularia*) se relocalizaron de un sitio en Santa Clara, California, a dos sitios aproximadamente 31 km al sur en marzo de 1990. Diez tecolotes se atraparon a mediados de Febrero y se liberaron de aviarios a mediados de marzo tres y cuatro semanas despues de captura. Se suplemento la alimentacion de las aves desde el dia de captura, y la cantidad de alimento se redujo gradualmente hasta zero. Monitoreamos movimientos locales de los diez tecolotes. Dos parejas de tecolotes se reproducieron exitosamente en dos sitios de relocalizacion. Una pareja produjo seis polluelos dos de los cuales sobrevivieron hasta volantones. El segundo par produjo huevos y pollos pero el nido fallo debido a depredacion. Otras dos parejas atentaron reproduccion (construyeron nidos) pero el macho de un par fue matado por un depredador antes de la postura de huevos y el segundo par abandono el sitio de recolonizacion y regresaron al sitio de captura. Seis tecolotes permanecieron en el sitio de relocalizacion en 1991 y dos tecolotes estaban presentes en 1992. Un par de tecolotes atentaron anidar en el sitio hasta 1994. Aunque los sitios de relocalizacion deberian de haberse manejado a largo plazo para los tecolotitos enanos estos planes de manejo no se siguierion y los tecolotes se dipsersaron para fines de 1991. Este estudio indico que los tecolotitos enanos pueden ser relocalizados exitosamente si se mueven a principios de la epoca reproductiva.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) is a small, terrestrial owl noted for its ability to coexist with humans in a variety of urban and semi-urban environments.

Once common, or even abundant locally, burrowing owls have declined over the last few decades throughout much of California (Grinnell and Miller 1944, McCaskie et al. 1979, Garrett and Dunn 1981). Population declines have been attributed to land development, cattle ranching, control of rodents, prairie dogs (*Cynomys* sp.), badgers (*Taxidea taxus*), and other burrowing animals, and vehicle strikes (Martell 1990, K. McKeever pers. comm.).

One potential solution to avoid increasing impacts to owls has involved relocating owls from impact areas to appropriate habitat elsewhere. Active relocation refers to physically trapping and moving owls from one location to another. Some relocations have been successful in that viable populations have been established (Dyer 1991).

Of eight previous relocations in California, three occurred in the fall, two in the spring, and the time of year is unknown for the other three (Feeney 1993). Of the three fall relocations, only one (using hacking aviaries) was moderately successful, with two of six owls remaining and breeding on site for up to three years (Harris 1987). Birds released during two spring relocations returned to the original site within one month of release (Feeney 1993). My study was designed to test the hypothesis that the timing of relocation may strongly influence whether birds stay on a relocation site.

METHODS

The capture site was a 24.3-ha parcel of land owned by the Mission College Foundation. The parcel will potentially be developed and is adjacent to busy freeway and surface streets in Santa Clara, California (Fig. 1).

A survey was conducted in December 1989 at the Mission College site to determine the number of owls to be trapped and the locations of their burrows. Two sites approximately 31 km to the south of the capture site were selected for relocating birds. These sites were on property owned by IBM Corporation, and both were designated as open space. One of the two sites is at the Santa Teresa Laboratory (STL), a 48.5-ha portion of a 478-ha parcel of land located north of Bailey Avenue and west of Highway 101. The second site, the Almaden Research Center (ARC) is a 280-ha parcel near Bernal Road. The relocation site at STL, at an elevation of 76 m, in the Santa Teresa Hills, is at the edge of an alluvial flood plain bordered to the southwest by oak woodland and to the southeast by agricultural fields. The site is valley grassland modified by agriculture. Prune and almond trees occupy part of the eastern and northeastern portion of the agricultural area. During the study, the site was managed as a hayfield, and red oats (*Avena* sp.) were planted in November and harvested in May. Following the harvest, the field was disked and left fallow between June and November. The herbicide 2,4-D was used on the crop to kill broadleaf weeds and field mustard (*Brassica rapa*). The farmer also hired a licensed pest control specialist on a yearly basis during the summer to control ground squirrels on the property. The specialist placed gas pellets (fumigants) in burrows, which were then closed. The farmer agreed not to control the ground squirrels in 1990 to prevent potential harm to burrowing owls (R. Lester pers. comm.). The ARC site, at an elevation of 256 m, is on serpentine rock, and contains grass species typical of serpentine grasslands. The site had been grazed by cattle continuously between the 1800s and 1987 (James A. Roberts Associates, Inc. undated). Although burrows of California ground squirrels (*Spermophilus beecheyi*) were present at both sites, artificial burrows were installed to provide additional nesting locations. Artificial burrows also provided a more controlled situation than ground squirrel burrows, whose configurations and occupancy could not be determined easily.

Santa Teresa Laboratory (STL). The area selected for nest sites is limited by agriculture. We set aside several sites with traditionally low yields for installation of artificial burrows and mounds. Artificial burrows generally followed the design described by Collins and Landry (1977). We installed four nest boxes approximately 3 m apart along a gently sloping hillside. Additional nest boxes were installed to allow for dispersal of owls following release. Each nest box was constructed from 2.5 cm thick redwood planks. The outside dimensions of each nest box were 40.6 cm × 30.5 cm × 30.5 cm, and the inside dimensions were 35.5 cm × 25.4 cm × 25.4 cm. The bottom of the box was open to the ground, and the top was secured by wood screws to allow for future observation and banding of nestlings. One 10 cm diameter hole was cut into the lower edge of two adjacent sides of each box. Two 10.2-cm diameter, 1.8 m long, corrugated, perforated PVC sewer drain pipes were fitted into each of the two holes in the box. Nest boxes were buried approximately 0.3 m below the ground surface, and 15–20 cm of dirt were mounded on top of each box. Hacking aviaries, with dimensions of 3 m × 3 m × 1.2 m, were constructed linearly with common walls. Aviary frames were made of 5 cm × 5 cm fir stakes. Heavy-duty black polyethylene marine netting (ADPI Enterprises Inc., Philadelphia, PA) with 1.2-cm mesh size was stapled to the sides and tops of frames. A feeding door, with dimensions of 41 cm × 51 cm was also secured to a top corner of each aviary. A section of 1.2 m wide chicken wire, folded in half, was attached to the sides of the aviaries from ground level up to a height of 0.6 m, then staked to the ground around the base of the aviaries. The chicken wire was intended to discourage mammalian predators, such as foxes (*Vulpes* sp.) or coyotes (*Canis latrans*) from digging under the aviary frames.

Twelve additional mounds were created in grassland. Mounds were spaced at least 31 m apart. Eight additional nest boxes were buried at ground level or above within dirt/debris mounds dumped along a grassy strip adjacent to Bailey Avenue. Four additional mounds were created with no nest boxes, to allow ground squirrels to create natural burrows.

Almaden Research Center (ARC). We installed a single artificial burrow and aviary with the same dimensions as those used at the STL (above) on the site at the base of a gently sloping hillside in the western corner of the agricultural area. Following a predator attack of the nest box in July, we reburied the nest box so that the top of the box was even with the ground surface. We secured the lid using wood screws and placed several large rocks on top of the earthen mound covering the nest box. We stretched heavy wire between tent stakes, which were driven into the ground on either side of the two plastic tunnel tubes to guard against further predation. The newly-strengthened nest box was tested the following day, when a predator unsuccessfully attempted to unearth the tubes. We installed two additional artificial burrows (each with one nest box) at the ARC site in early August to provide additional refugia for a second group of owls released on site. The nest boxes were 45–60 m from the original artificial burrow placed at that site.

Trapping. Between 15–21 February 1990 we placed noose carpets and Bal-chatri traps near burrows where pairs had been previously observed. Observers waited in vehicles at some distance and checked traps approximately once per half-hour. We removed captured birds immediately and placed them in standard cardboard pet carrying boxes.

Transfer to Rehabilitation Facility. We transported all captured owls to the Santa Clara Valley Humane Society. A rehabilitator experienced with burrowing owls examined each owl externally for parasites and diseases and tested a stool sample from each bird for internal parasites, such as *Capillaria.* Two of four owls captured carried feather lice (Laemobothriidae). One owl was treated for capillaria for 5 days, and one owl had infections on the toes and forehead which were treated with betadine and fenbendazole. We then transferred owls testing negative for internal parasites to another aviary for 13–15 d. We temporarily confined owls as an attempt to disrupt homing mechanisms prior to relocation. The approximate dimensions of the aviary were 3 m × 4.3 m × 2.4 m. We buried two nest boxes with approximate dimensions of 30–35 cm on a side in the ground with PVC tubes connecting them to the outside. We placed two perches along each of two sides of the cage, approximately 1.5 m above the ground. The inside walls and ground of the aviary had been disinfected with a solution of bleach and disinfectant prior to introducing the owls. We transferred three owls on 20 February and one owl on 22 February. We left live commercially-raised mice (B & K Universal, Fremont, CA) and crickets in the aviary daily and provided drinking water in a shallow bowl.

Relocation, Feeding, and Monitoring. We transferred owls to the two relocation sites on 5 March 1990, and placed each pair in a separate aviary for 10 d. We visited the site periodically to determine numbers and locations of owls at both sites, maintain burrows and provide supplemental mice. We removed old or rotting mouse carcasses from the immediate burrow entrances to avoid attracting predators to the site, collected regurgitated pellets during feeding visits, and periodically examined them to determine percentage of "wild" food the owls were procuring. We used this information to adjust the amount of supplemental food.

At the STL site, we supplementally fed the eight owls two mice per owl per day during the captivity period. After ten days, the hacking aviaries were removed, and owls were allowed to move freely. We left frozen mice inside burrow tunnel entrances to discourage predators, such as northern harriers (*Circus cyaneus*) from eating the mice. We fed and observed owls in the late afternoon, or evening, when they were most likely to be observed. We changed this feeding protocol after 10 April, when owls were observed feeding on mice during morning hours and were observed outside burrows at all times of the day. Two mice per owl per day were left for another five weeks, unless mice from a previous feeding were still present. We then fed owls three mice per pair for 12 d, followed by two mice per pair for one wk, and one mouse per pair every four d for a period of 20 d. The frequency of supplemental feeding increased to every other day when nestlings were discovered at one nest.

Additional Owl Releases. We relocated six additional owls on 21 June and released five fledged young on 19 September at the STL site. We also relocated six owls (three adults and three juveniles) to the ARC site on 7 August. All additional owls were hacked out in aviaries prior to release and fed in a similar fashion to the original five pairs.

Banding, Site Maintenance, and Follow-up Visits. We unearthed the four nest boxes at STL and one nest box at ARC on 15 March to determine nesting progress. We cleaned out unoccupied burrows and replaced nest box lids. One nest box was reopened on 5 June to band nestlings prior to their emergence from the burrow. We trimmed weeds growing around the four artificial burrows by hand and with a sickle bar mower (in June). The red oat crop was harvested in early May and the field was disked (excluding the burrow mounds). We revisited the STL site on 6 February 1991 to determine the number of owls remaining on the site. We visited the STL site on 11 April and the ARC site on 25 April 1992 to assess the number of owls on the sites and the integrity of the burrow sites.

RESULTS

Trapping Efficiency. The first group of six owls was captured at Mission College between 0545–1030 H on 15 February (trapping efficiency of 1 owl per 1.26 h). We captured four owls using noose carpets and two owls with Bal-chatri traps. We captured four additional owls on 21 February between 0530–0912 H. We captured two owls with Bal-chatri traps and two with noose carpets (trapping efficiency of 1 owl per 1.07 h).

Male-male interactions. Within one or two hours of their release from the aviaries, male owls from STL pairs 1, 2, and 3 were observed copulating with their mates. We also observed aggression between males of different pairs. Approximately 45 min after owls had emerged from burrows, the male of pair 2 attacked and briefly pinned the pair 1 male on the ground. The male of pair 1 subsequently attacked the pair 2 male after approximately 30 min. Fifteen min later, the males from pairs 2 and 3 were fighting. This pair engaged in another aggressive encounter approximately 65 min later.

Reproductive Success. Four of the five relocated pairs attempted breeding and produced eight nestlings and five eggs. At least two of the eight nestlings fledged at the STL site.

Pair 1 had begun lining its nest at artificial burrow A. When the nest box was checked on 15 May, some cut grass, cow dung, pellets, and 18 dead mice were found inside. The male, who had become relatively tame, was observed outside the burrow until at least 12 April. Owl feather remains were found near the burrow entrance on approximately 15 April and it is assumed that the male was killed by a predator. The female was observed at the original nest burrow until 18 April. Pair 1 remained at the relocation site longer than one month, and the female remained for an additional seven weeks.

Pair 2 originally occupied burrow B and remained there for more than one month. This pair used two burrows initially occupied by pair 4, and successfully nested. On 15 May, two months after release, four downy nestlings (approximately 10 cm in length), with eyes still closed, plus a single unhatched egg were observed in the burrow. We estimated that the young hatched between 9–17 May, and the four nestlings were between 2- and 4-d-old. By 5 June the female had laid a sixth egg, and all six young were banded with USFWS bands and colorbands. At least two of the young fledged and were observed on site through 24 August.

Pair 3 demonstrated breeding behavior (copulation) and remained at the relocation site for ten days following release. The pair was not observed thereafter.

Pair 4 initially occupied burrow D after release from the hacking aviary, but then moved to burrow F after two days, where they remained until 16 April (nearly four wk). We observed the pair using three adjacent artificial burrows (H, I, and J) south of the original four nest burrows. The pair showed evidence of courtship behavior and nest-building, but by 8 June, the female was often observed outside the burrow entrance, indicating that she was not incubating. The pair remained together through 21 July. The male of pair 4 joined a female who had been introduced to the site with 5 young on 21 June. The female returned to Mission College sometime during the next two years and was observed at that site with five young in 1992.

Pair 5 began foraging about two hours following release. The pair remained on site and successfully bred and produced three nestlings and five eggs. Two freshly killed meadow mice (*Microtus californicus*) were observed in the nest box. A predator (probably a coyote [*Canis latrans*]) dug up and opened the nest box one day after the nest check. The pair remained on site until 12 June, about one week following the destruction of their nest. The male remained on site for at least two additional months.

In 1991, one year following relocation, a pair of owls attempted to nest at the ARC site in a natural ground squirrel burrow (A. Erickson pers. comm.), and a single owl was also observed near the release site during May of that year. At least one owl has been reported at the ARC site in 1992, 1993, and 1994. The bird observed in fall of 1994 appeared to be a resident (vs. a migrant), due to the amount of whitewash and other signs around its three burrows (D. Hildebrand pers. comm.).

Mortality. Feather remains were found near the burrow of pair 1 on or about 15 April, and the male was assumed to have been killed by a predator. The day following a check of the nest box of pair 5 (ARC site) for nesting progress, a predator dug out the nest box, opened the lid and removed eggs and nestlings. The predator was likely a coyote or red fox (*V. vulpes*).

Dispersal. The pair 1 female, whose mate had been killed by a predator, was observed back at the Mission College site on 8 June, approximately 2.5 mo following release. She paired with a two-year-old (or older) male owl (banded in 1988), but did not breed in 1990. Pair 2 remained at the relocation site through the 1990 breeding season.

Pair 3 (from burrow C) began exploring burrow G after four days, although the male was still observed at the original burrow on the fourth day. The pair moved to and remained at burrow G until 25 March, 10 d following release but was not observed again. The plastic tunnel pipes to burrow G had been partially excavated by a ground predator on 23 March. Coyote scat was found near the burrow entrance on 27 March.

Pair 4 remained at the relocation site during 1990, but did not breed. The female was not observed after 21 July at the relocation site, but was later observed (in 1992) at the Mission College capture site.

The pair 5 female was observed at the Mission College site on 19 July (37 d after it was last observed at the ARC site). The female was observed two years later at Mission College (April–August 1992) with two fledged young. Her right eye was abscessed, possibly as a result of a foxtail (*Bromus* sp.) puncture. The female was later found at least 1.6 km from the site, where she had apparently been struck by a vehicle, and was transported to the Santa Clara Valley Humane Society. The bird eventually died of internal injuries.

The owls that remained at the STL relocation site, some of which could have been young of the

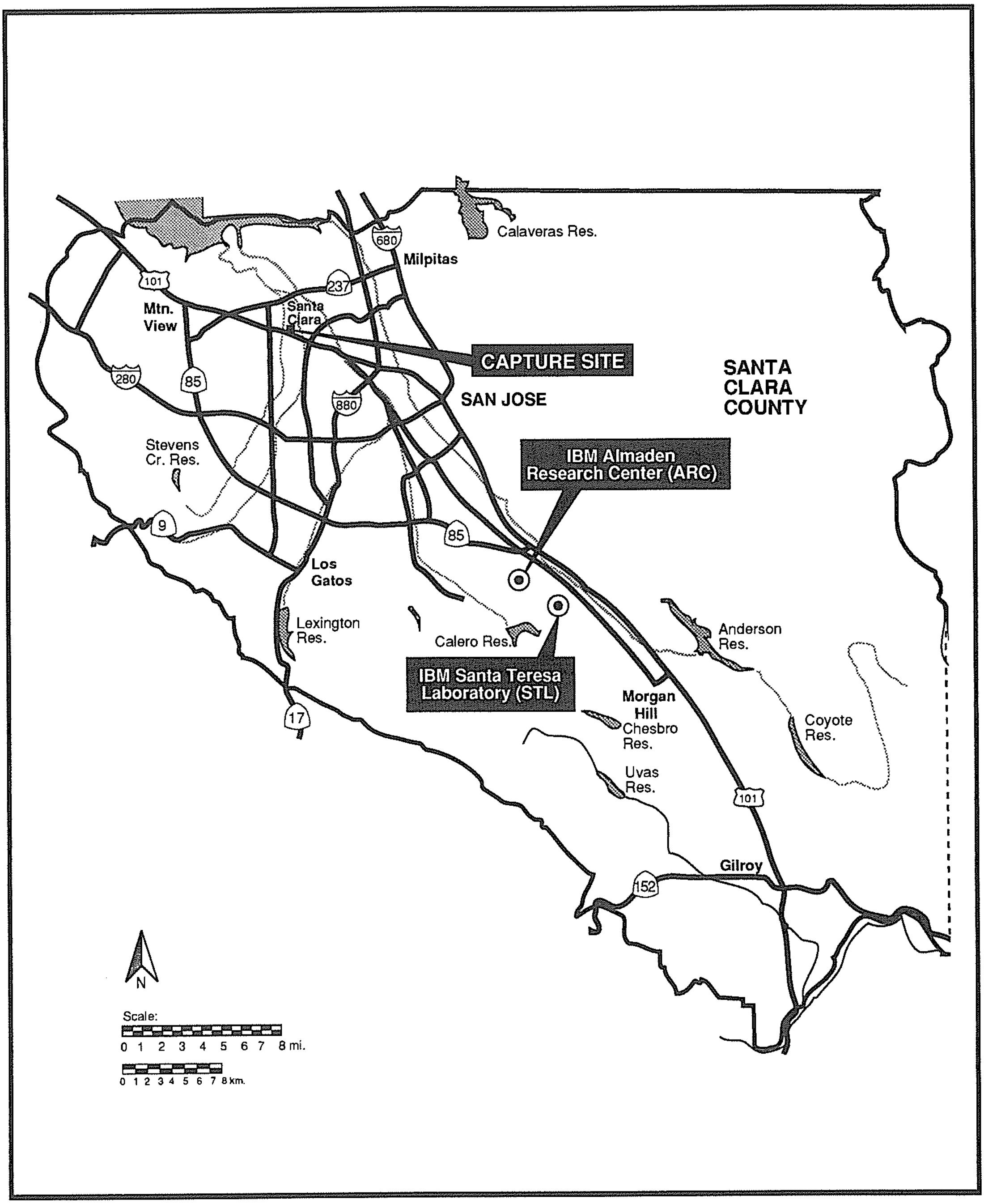

Figure 1. Location of capture site and relocation sites, San Jose, Santa Clara County, California.

above pairs, were supplementally fed through 29 November. The highest number of owls observed between September and November was six on 8 November. Two of the six appeared to be "paired."

DISCUSSION

This study represented one of the few attempts to relocate burrowing owls at the onset of the breeding season. Previous studies (e.g., Feeney 1997, H.T. Harvey and Associates 1993, Harris 1987) attempted relocation after the breeding season (primarily during the fall dispersal period). The most successful relocations to date involved moving dependent young with adults over a period of four to eight years (Dyer 1991). Four pairs of owls attempted breeding on site, and two pairs successfully produced young.

Even with the successful breeding of two pairs, there was some mortality and homing behavior. One male owl (pair 1) was killed by a predator. His mate returned to the Mission College capture site within two months of the male's death. The nesting failure of pair 5 was due to predation resulting from inadequate closure of the nest box. The female of this pair returned to Mission College within 28 d and bred the following season. Pair 2 produced 6 nestlings, of which at least two fledged. It is unclear how many, if any, survived to the following breeding season.

Two owls from STL and one owl from ARC returned to the relocation site within two years of release. All three were females who had failed at a nesting attempt, either through loss of eggs and young, loss of a mate, or unknown causes.

The STL site was not managed as habitat for burrowing owls. With proper habitat management, the owls would probably have persisted for a longer period and in higher numbers. Limited burrowing owl habitat was available at the ARC site, so only one pair of owls was initially moved to that site. However, it appears that at least one owl has remained at that site for four years. IBM Corporation had intended to follow a habitat management plan, which included plans for enhancing the STL site for burrowing owls. However, due to unforeseen circumstances, IBM was not able to follow the management plan. The agricultural regime of planting, harvesting, and disking that had been practiced for several years was continued during the study period. As previously noted, the site was disked and left fallow between June and November, the period when nestlings and fledglings would require the most amount of food for growth. The owls may have moved off site due to the lack of food during the critical nestling and fledgling period. The productivity of the land also may have been too low to support a large population of owls.

Methods for reducing territorial interactions need to be examined. Although additional artificial burrows were installed around the perimeter of the habitat available for owls, the artificial burrows at the STL site were placed too close to one another. This probably enhanced initial defensive encounters between males. Two males exhibited aggressive interactions on the first day of release from aviaries. Two pairs moved away from the original four-burrow complex to nearby burrows.

The selection and preparation of new nest burrows, and holding birds in captivity probably delayed the onset of egg-laying. Future relocations should consider decreasing the period in captivity, and increasing the distance between artificial burrows to at least 60 m (average of internest distances reported by Thomsen 1971).

We fed the owls more mice than necessary. Observers were not aware that owls were storing mice in large quantities until nest boxes were opened. The relocated birds from STL stored a large number of laboratory mice during 2.5 mo. One burrow contained 102 decaying mice, and five burrows contained 259 mice. Caching large quantities of food items may have attracted predators to the site. Reduction in the supplemental feeding may reduce predation.

The relocated owls also may have experienced unfamiliar predators, such as coyotes, red foxes, striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), bobcats (*Lynx rufus*), and gopher snakes (*Pituophis catenifer*), although red-tailed hawks (*Buteo jamaicensis*) and feral cats were common predators at the Mission College site.

In conclusion, relocations can work with improved techniques. This study demonstrated that birds moved prior to the initiation of egg-laying will breed successfully and remain at a new site less than 32 km distant. With proper land management, relocated birds may be able to sustain viable populations. Future research should focus on relocation site suitability and possible ways to reduce predation.

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I wish to thank the following persons for their advice, help in trapping and relocating owls, or for intermediate facilities: Craig Kuziel and Colleen Lenihan for their talents during aviary construction and trapping; Joan Priest and Jean Young for their care and treatment of the owls; and Janis T. Buchanan, Armand Gonzales (CDFG), Brenda Johnson, Susan Lyman, Ray Lester, Richard Reisman, Elsie Richey, Ken Ryan, Scott B. Terrill, and George Wade. I would also like to thank the following volunteers from IBM ARC and STL for giving so freely of their time and enthusiasm: Matt Anderson, John Artim, Perry Babel, Sheila Barclay, Irene Beardsley, Brenda Brown, Ray Dias, Rich Ehrhart, Allyn Erickson, Earl Hames, Dave Hildebrand, Mary Lehner, Dave Lopez, Bill Lundgren, Alan Neal, Dieter Thiel, Tom Maxson, Lance Porter, Berne Schoonmaker, Rick Stees, Stanley Taylor and Gloria Thompson. I am grateful to IBM Corporation for providing a relocation site, funds and manpower for building aviaries, and providing feeder mice. I also wish to thank Scott Terrill, Michael Newcomer, Karen Steenhof, and Jeff Lincer for reviewing the paper and providing helpful comments.

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APPENDIX A

A BIBLIOGRAPHY ON THE BURROWING OWL (*SPEOTYTO CUNICULARIA*)

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BACKGROUND

One might ask, in this day and age of electronic information retrieval, why we are producing a hard copy of a bibliography on just a single species of owl? We offer in reply, that even though professional researchers within university systems or within governmental agencies in the industrial world may have access to such "necessities," for much of the rest of the world that is still a luxury beyond the reach of those who could make use of it. The burrowing owl (*Speotyto cunicularia*) is found throughout much of the Western Hemisphere from southcentral and southwestern Canada to Tierra del Fuego. While the range of the race found in Florida (*floridana*) has been expanding due to forest clearing and draining activities, there are numerous other places where the species is declining. Because it is so "tied to the land" with its nesting habitats, this trend could reasonably be expected to not only continue but even increase at a greater rate as the human population continues to increase and agricultural practices intensify to feed the burgeoning human population. It is for these and other reasons that this bibliography was produced to assist researchers in uncovering the basic biology of this species and land managers in devising plans that can maximize the conservation of this species. Thus far, two races of the species have been eliminated (i.e., *guadeloupensis* from Guadeloupe and/or Marie Galante Island and *amaura* from Antigua in the West Indies). Both disappeared at the end of the nineteenth century at about the same time and shortly after the introduction of the mongoose by man (Greenway 1967).

METHODS

One should note that no bibliography is ever complete. All known and available literature databases and bibliographies have been searched. The databases include those information systems of the Raptor Research and Technical Assistance Center (RRTAC) created by Richard Olendorff, Karen Steenhof and others and **The Field Ornithology Index** (years 1984 through mid-1990 obtained on diskettes from the compiler John Kennington of Tulsa, Oklahoma). The **Science Citation Index** (January 1985–June 1992), **Dissertation Abstracts** (1861–June 1992), **Periodical Abstracts** and **Newspaper Abstracts** were all searched (from CD-ROM) at the Science Library, University of Kansas Libraries, Lawrence. Also searched via Lockheed's **Dialog** were **Biosis Previews, Books in Print, Life Science Collections, SciSearch** and **Zoological Record** by Bill Markle, Reference Librarian for York College of Pennsylvania. Bibliographies checked included those by Clark, Smith and Kelso (1978), Dunbar (1982), Knight (1979) and Olendorff (1989). Abstracts for Raptor Research Foundation annual conferences were checked for the years 1977–1992. Journal title abbreviations were taken from *Serial Sources for the BIOSIS Previews®*, Volume 1991.

It is our intent to produce a working bibliography; that is, one that is cross-referenced at a later date; hence, there is still ample time for those who know of other appropriate references. Especially helpful are reprints which allow some form of keywording to be created. Please send them to: Richard J. Clark, Burrowing Owl Bibliography, c/o Department of Biology, York College of Pennsylvania, York, PA 17405-7199 U.S.A.

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ing owl or *Speotyto cunicularia* or *Athene cunicularia* appeared in the title and/or the keywords of that specific article. A grant from the Research and Publications Committee of York College of Pennsylvania's Faculty Senate is hereby gratefully acknowledged, as is support from Biosystems Analysis, Inc. and Sweetwater Environmental Biologists, Inc.

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APPENDIX B

BURROWING OWL SURVEY PROTOCOL AND MITIGATION GUIDELINES

Prepared by:
The California Burrowing Owl Consortium

Editor's Note: The California Burrowing Owl Consortium prepared the "Burrowing Owl Survey Protocol and Mitigation Guidelines" in response to the need for more uniform methods of conducting owl surveys and to promote more consistent procedures in mitigating impacts to burrowing owls from development projects. The Consortium is a group of approximately 60 biologists and citizens interested in burrowing owl conservation and management in the San Francisco Bay area. This document was submitted to the California Department of Fish and Game (CDFG) for review and to any interested party who requested information regarding survey methods or mitigation strategies. For more information, updates, or to provide input to these evolving guidelines, contact: Mr. Jack Barclay, BioSystems Analysis, Inc., 303 Potrero Street, Suite 29-203, Santa Cruz, California 95060, (408) 459-9100. For information on CDFG's Staff Report on Burrowing Owl Mitigation guidelines, please contact Mr. Ron Rempel, CDFG, 1416 9th Street, Room 1341, Sacramento, California 95814, (916) 654–9980.

Background

The California Burrowing Owl Consortium developed the following Survey Protocol and Mitigation Guidelines to meet the need for uniform standards when surveying burrowing owl (*Speotyto cunicularia*) populations and evaluating impacts from development projects. The California Burrowing Owl Consortium is a group of biologists in the San Francisco Bay area who are interested in burrowing owl conservation. The following survey protocol and mitigation guidelines were prepared by the Consortium's Mitigation Committee. These procedures offer a decision-making process aimed at preserving burrowing owls in place with adequate habitat.

California's burrowing owl population is clearly in peril and if declines continue unchecked the species may qualify for listing. Because of the intense pressure for development of open, flat grasslands in California, resource managers frequently face conflicts between owls and development projects. Owls can be affected by disturbance and habitat loss, even though there may be no direct impacts to the birds themselves or their burrows. There is often inadequate information about the presence of owls on a project site until ground disturbance is imminent. When this occurs there is usually insufficient time to evaluate impacts to owls and their habitat. The absence of standardized field survey methods impairs adequate and consistent impact assessment during regulatory review processes, which in turn reduces the possibility of effective mitigation.

These guidelines are intended to provide a decision-making process that should be implemented wherever there is potential for an action or project to adversely affect burrowing owls or the resources that support them. The process begins with a four-step survey protocol to document the presence of burrowing owl habitat, and evaluate burrowing owl use of the project site and a surrounding buffer zone. When surveys confirm occupied habitat, the mitigation measures are followed to minimize impacts to burrowing owls, their burrows and foraging habitat on the site. These guidelines emphasize maintaining burrowing owls and their resources in place rather than minimizing impacts through displacement of owls to an alternate site.

Each project and situation is different and these procedures may not be applicable in some circumstances. Finally, these are not strict rules or requirements that must be applied in all situations. They are guidelines to consider when evaluating burrowing owls and their habitat, and they suggest options for burrowing owl conservation when land use decisions are made.

Section 1 describes the four phase Burrowing Owl Survey Protocol. Section 2 contains the Mitigation Guidelines. Section 3 contains a discussion of various laws and regulations that protect burrowing owls and a list of references cited in the text.

We have submitted these documents to the California Department of Fish and Game (CDFG) for review and comment. These are untested procedures and we ask for your comments on improving their usefulness.

SECTION 1: BURROWING OWL SURVEY PROTOCOL

Phase I: Habitat Assessment

The first step in the survey process is to assess the presence of burrowing owl habitat on the project site including a 150-m (approx. 500 ft.) buffer zone around the project boundary (Thomsen 1971, Martin 1973) (Figure 1).

Burrowing Owl Habitat Description. Burrowing owl habitat can be found in annual and perennial grasslands, deserts, and scrublands characterized by low-growing vegetation (Zarn 1974). Suitable owl habitat may also include trees and shrubs if the canopy covers less than 30% of the ground surface. Burrows are the essential component of burrowing owl habitat: both natural and artificial burrows provide protection, shelter, and nests for burrowing owls (Henny and Blus 1981). Burrowing owls typically use burrows made by fossorial mammals, such as ground squirrels (*Spermaphilus beecheyi*) or badgers (*Taxidea taxus*), but also may use man-made structures, such as cement culverts; cement, asphalt, or wood debris piles; or openings beneath cement or asphalt pavement.

Occupied Burrowing Owl Habitat. Burrowing owls may use a site for breeding, wintering, foraging, and/or migration stopovers. Occupancy of suitable burrowing owl habitat can be verified at a site by an observation of at least one burrowing owl, or, alternatively, its molted feathers, cast pellets, prey remains, eggshell fragments, or excrement at or near a burrow entrance. Burrowing owls exhibit high site fidelity, reusing burrows year after year (Rich 1984, Feeney 1992). A site should be assumed occupied if at least one burrowing owl has been observed occupying a burrow there within the last three years (Rich 1984).

The Phase II burrow survey is required if burrowing owl habitat occurs on the site. If burrowing owl habitat is not present on the project site and buffer zone, the Phase II burrow survey is not necessary. A written report of the habitat assessment should be prepared (Phase IV), stating the reason(s) why the area is not burrowing owl habitat.

PHASE II: BURROW SURVEY

1. A survey for burrows and owls should be conducted by walking through suitable habitat over the entire project site and in areas within 150 m (approx 500 ft.) of the project impact zone. This 150-m buffer zone is included to account for adjacent burrows and foraging habitat outside the project area and impacts from factors such as noise and vibration due to heavy equipment which could impact resources outside the project area.

2. Pedestrian survey transects should be spaced to allow 100% visual coverage of the ground surface. The distance between transect center lines should be no more than 30 m (approx. 100 ft.), and should be reduced to account for differences in terrain, vegetation density, and ground surface visibility. To efficiently survey projects larger than 100 acres, it is recommended that two or more surveyors conduct concurrent surveys. Surveyors should maintain a minimum distance of 50 m (approx. 160 ft.) from any owls or occupied burrows. It is important to minimize disturbance near occupied burrows during all seasons.

3. If burrows or burrowing owls are recorded on the site, a map should be prepared of the burrow concentration areas. A breeding season survey and census (Phase III) of burrowing owls is the next step required.

4. Prepare a report (Phase IV) of the burrow survey stating whether or not burrows are present.

5. A preconstruction survey may be required by project-specific mitigations no more than 30 days prior to ground disturbing activity.

PHASE III: BURROWING OWL SURVEYS, CENSUS AND MAPPING

If the project site contains burrows that could be used by burrowing owls, then survey efforts should be directed toward determining owl presence on the site. Surveys in the breeding season are required to describe if, when, and how the site is used by burrowing owls. If no owls are observed using the site during the breeding season, a winter survey is required.

Survey Methodology. A complete burrowing owl survey consists of four site visits. During the initial site visit examine burrows for owl sign and map the locations of occupied burrows. Subsequent observations should be conducted from as many fixed points as necessary to provide visual coverage of the site using spotting scopes or binoculars. It is important to minimize disturbance near occupied burrows during all seasons. Site visits must be repeated on four separate days. Conduct these visits from two hours before sunset to one hour after or from one hour before to two hours after sunrise. Surveys should be conducted during weather that is conducive to observing owls outside their burrows. Avoid surveys during heavy rain, high winds (> 32 kmp), or dense fog.

Nesting Season Survey. The burrowing owl nesting season begins as early as 1 February and continues through 31 August (Thomsen 1971, Zarn 1974). The timing of nesting activities may vary with latitude and climatic conditions. If possible, the nesting season survey should be conducted during the peak of the breeding season, between 15 April and 15 July. Count and map all burrowing owl sightings, occupied burrows, and burrows with owl sign. Record numbers of pairs and juveniles, and behavior such as courtship and copulation. Map the approximate territory boundaries and foraging areas if known.

Survey for Winter Residents (non-breeding owls). Winter surveys should be conducted between 1 December and 31 January, during the period when wintering owls are most likely to be present. Count and map all owl sightings, occupied burrows, and burrows with owl sign.

Surveys Outside the Winter and Nesting Seasons. Positive results (i.e., owl sightings) outside of the above survey periods would be adequate to determine presence of owls on site. However, results of these surveys may be inadequate for mitigation planning because the numbers of owls and their pattern of distribution may change dur-

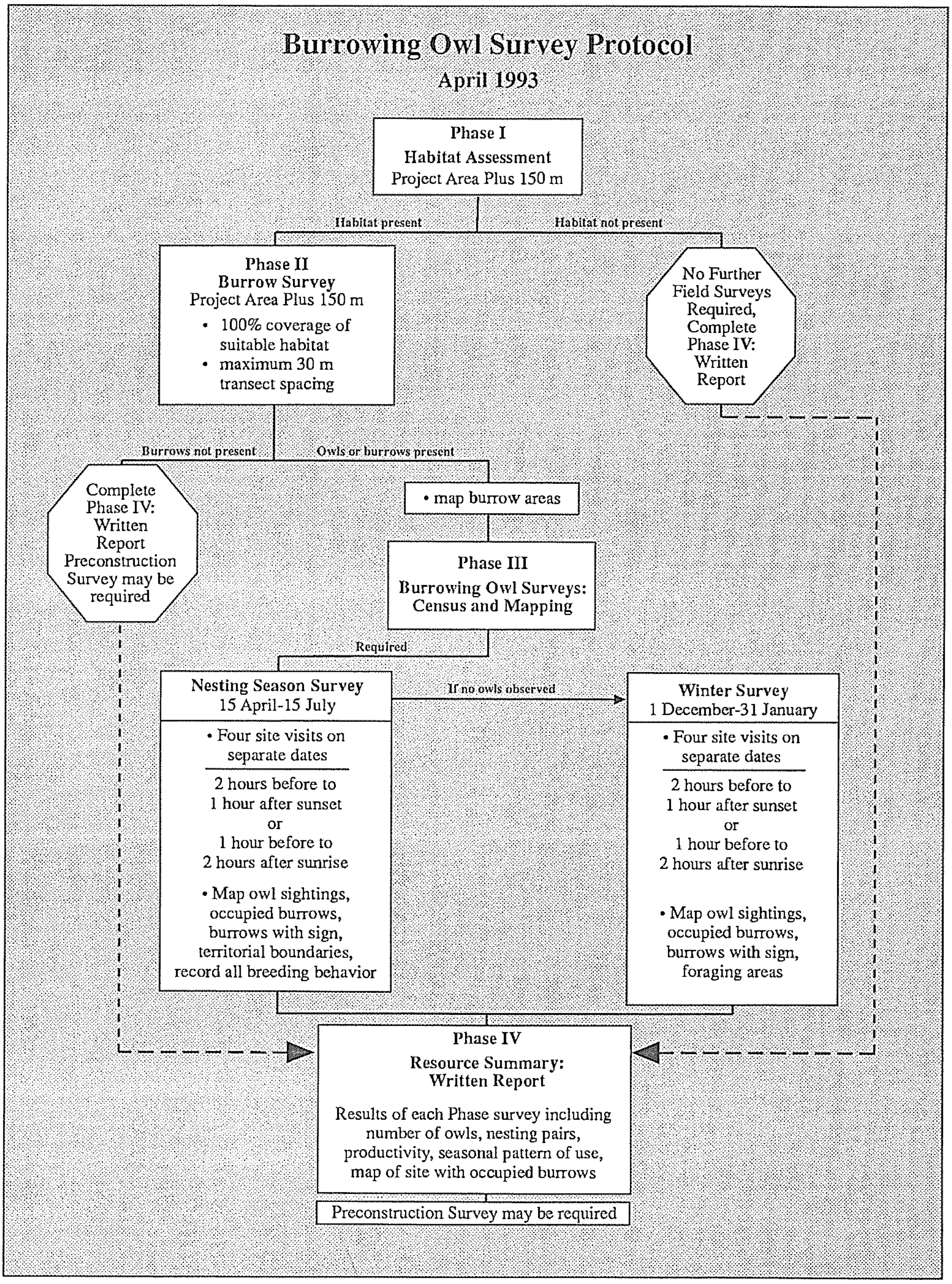

Figure 1. Burrowing owl survey protocol.

ing winter and nesting seasons. Negative results during surveys outside the above periods are not conclusive proof that owls do not use the site.

Preconstruction Survey. A preconstruction survey may be required by project-specific mitigations and should be conducted no more than 30 d prior to ground disturbing activity.

PHASE IV: RESOURCE SUMMARY, WRITTEN REPORT

A report should be prepared for CDFG that gives the results of each Phase of the survey protocol, as outlined below.

Phase I: Habitat Assessment

1. Date and time of visit(s) including weather and visibility conditions; methods of survey.
2. Site description including the following information: location, size, topography, vegetation communities, and animals observed during visit(s).
3. An assessment of habitat suitability for burrowing owls and explanation.
4. A map of the site.

Phase II: Burrow Survey

1. Date and time of visits including weather and visibility conditions; survey methods including transect spacing.
2. A more detailed site description should be made during this phase of the survey protocol including a partial plant list of primary vegetation, location of nearest freshwater (on or within 1.6 km of site), animals observed during transects.
3. Results of survey transects including a map showing the location of concentrations of burrow(s) (natural or artificial) and owl(s), if present.

Phase III: Burrowing Owl Surveys, Census and Mapping

1. Date and time of visits including weather and visibility conditions; survey methods including transect spacing.
2. Report and map the location of all burrowing owls and owl sign. Burrows occupied by owl(s) should be mapped indicating the number of owls at each burrow. Tracks, feathers, pellets, or other items (prey remains, animal scat) at burrows should also be reported.
3. Behavior of owls during the surveys should be carefully recorded (from a distance) and reported. Describe and map areas used by owls during the surveys. Although not required, all behavior is valuable to document including feeding, resting, courtship, alarm, territorial, parental, or juvenile behavior.
4. Both winter and nesting season surveys should be summarized. If possible include information regarding productivity of pairs, seasonal pattern of use, and include a map of the colony showing territorial boundaries and home ranges.
5. The historical presence of burrowing owls on site should be documented, as well as the source of such information (local bird club, Audubon society, other biologists, etc.).

SECTION 2: BURROWING OWL MITIGATION GUIDELINES

The objective of these mitigation guidelines is to minimize impacts to burrowing owls and the resources that support viable owl populations. These guidelines are intended to provide a decision-making process that should be implemented wherever there is potential for an action or project to adversely affect burrowing owls or their resources. The process begins with a four-step survey protocol (see *Burrowing Owl Survey Protocol*) to document the presence of burrowing owl habitat, and evaluate burrowing owl use of the project site and a surrounding buffer zone. When surveys confirm occupied habitat, the mitigation measures described below are followed to minimize impacts to burrowing owls, their burrows and foraging habitat on the site. These guidelines emphasize maintaining burrowing owls and their resources in place rather than minimizing impacts through displacement of owls to an alternate site.

Mitigation actions should be carried out prior to the burrowing owl breeding season, generally from 1 February through 31 August (Thomsen 1971, Zarn 1974). The timing of nesting activity may vary with latitude and climatic conditions. Project sites and buffer zones with suitable habitat should be resurveyed to ensure no burrowing owls have occupied them in the interim period between the initial surveys and ground disturbing activity. Repeat surveys should be conducted not more than 30 d prior to initial ground disturbing activity.

DEFINITION OF IMPACTS

1. Disturbance or harassment within 50 m (approx. 160 ft.) of occupied burrows.
2. Destruction of burrows and burrow entrances. Burrows include structures such as culverts, concrete slabs and debris piles that provide shelter to burrowing owls.
3. Degradation of foraging habitat adjacent to occupied burrows.

GENERAL CONSIDERATIONS

1. Occupied burrows should not be disturbed during the nesting season, from 1 February through 31 August, unless the Department of Fish and Game verifies that the birds have not begun egg-laying and incubation or that the juveniles from those burrows are foraging independently and capable of independent survival at an earlier date.
2. A minimum of 16 hectares of foraging habitat, calculated on a 100-m (approx. 300 ft.) foraging radius around the natal burrow, should be maintained per pair (or unpaired resident single bird) contiguous with burrows occupied within the last three years (Rich 1984, Fee-

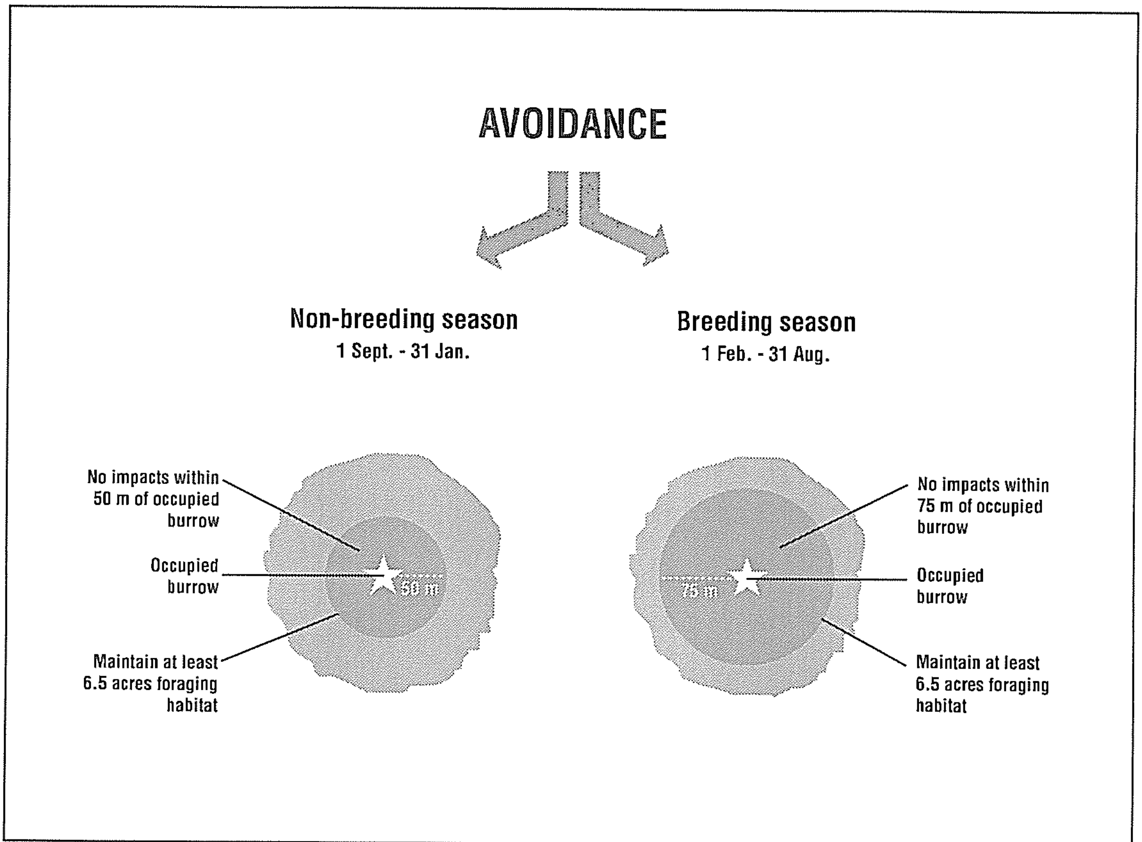

Figure 2. Avoidance area and necessary foraging habitat.

ney 1992). Ideally, foraging habitat should be retained in a long-term conservation easement.

3. When destruction of occupied burrows is unavoidable, burrows should be enhanced (enlarged or cleared of debris) or created (by installing artificial burrows) in a ratio of 1:1 in adjacent suitable habitat that is contiguous with the foraging habitat of the affected owls.

4. If owls must be moved away from the disturbance area, passive relocation (see below) is preferable to trapping. A time period of at least one week is recommended to allow the owls to move and acclimate to alternate burrows.

5. The mitigation committee recommends monitoring the success of mitigation programs as required in Assembly Bill 3180. A monitoring plan should include mitigation success criteria and an annual report should be submitted to the California Department of Fish and Game.

AVOIDANCE

Avoid Occupied Burrows. No disturbance should occur within 50 m (approx. 160 ft.) of occupied burrows during the non-breeding season of 1 September through 31 January or within 75 m (approx. 250 ft.) during the breeding season of 1 February through 31 August. Avoidance also requires that a minimum of 6.5 acres of foraging habitat be preserved contiguous with occupied burrow sites for each pair of breeding burrowing owls (with or without dependent young) or single unpaired resident bird (Figure 2).

MITIGATION FOR UNAVOIDABLE IMPACTS

On-site Mitigation. On-site passive relocation should be implemented if the above avoidance requirements cannot be met. Passive relocation is defined as encouraging owls to move from occupied burrows to alternate natural or artificial burrows that are beyond 50 m from the impact zone and that are within or contiguous to a minimum of 16 hectares of foraging habitat for each pair of relocated owls (Figure 3). Relocation of owls should only be implemented during the non-breeding season. On-site habitat should be preserved in a conservation easement and managed to promote burrowing owl use of the site.

Owls should be excluded from burrows in the immediate impact zone and within a 50 m (approx. 160 ft.)

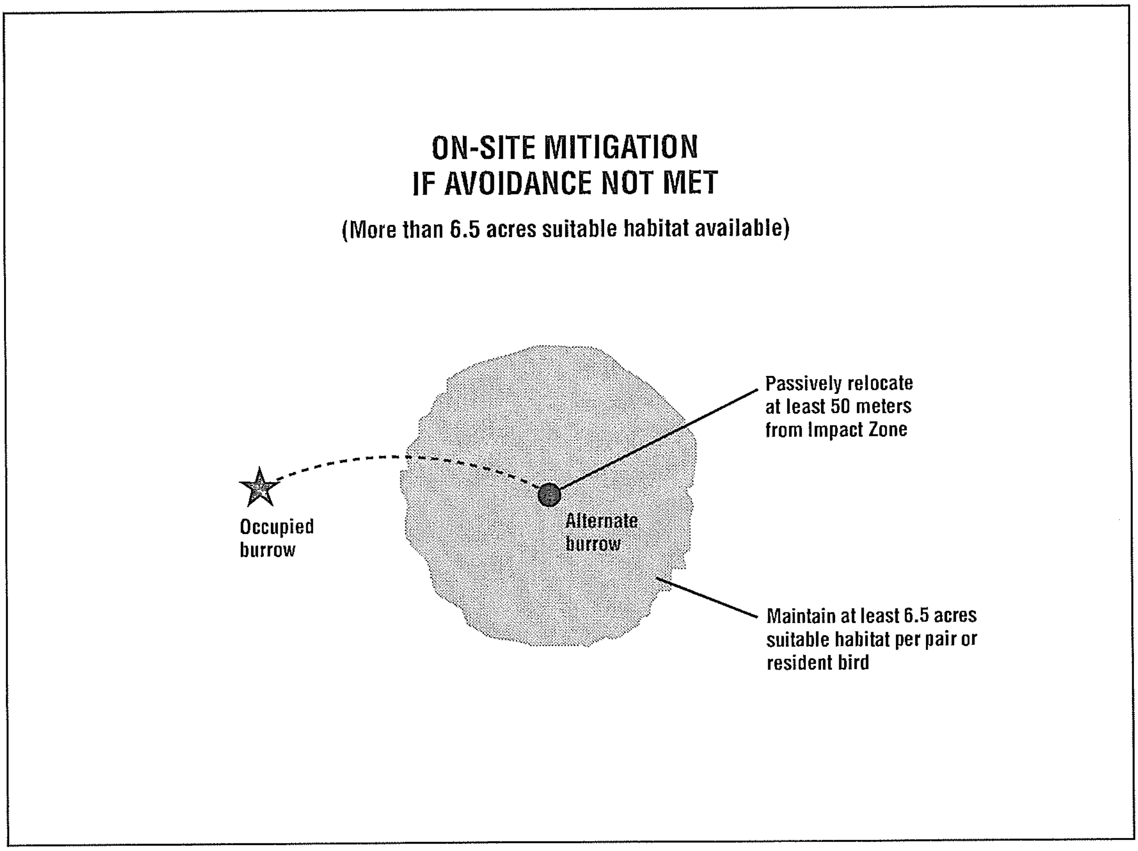

Figure 3. On-site mitigation.

buffer zone by installing one-way doors in burrow entrances. One-way doors should be left in place 48 h to ensure owls have left the burrow before excavation. One alternate natural or artificial burrow should be provided for each burrow that will be excavated in the project impact zone. The project area should be monitored daily for one week to confirm owl use of alternate burrows before excavating burrows in the immediate impact zone. Whenever possible, burrows should be excavated using hand tools and refilled to prevent reoccupation. Sections of flexible plastic pipe or burlap bags should be inserted into the tunnels during excavation to maintain an escape route for any animals inside the burrow.

Off-site Mitigation. If the project will reduce suitable habitat on-site below the threshold level of 6.5 acres per relocated pair or single bird, the habitat should be replaced off-site. Off-site habitat must be suitable burrowing owl habitat, as defined in the *Burrowing Owl Survey Protocol,* and the site approved by CDFG. Land should be purchased and/or placed in a conservation easement in perpetuity and managed to maintain suitable habitat. Off-site mitigation should use one of the following ratios:

1. Replacement of occupied habitat with occupied habitat: 1.5 times 6.5 (9.75) acres per pair or single bird.
2. Replacement of occupied habitat with habitat contiguous to currently occupied habitat: 2 times 6.5 (13.0) acres per pair or single bird.
3. Replacement of occupied habitat with suitable unoccupied habitat: 3 times 6.5 (19.5) acres per pair or single bird.

SECTION 3: LEGAL STATUS

The burrowing owl is a migratory bird species protected by international treaty under the Migratory Bird Treaty Act (MBTA) of 1918 (16 U.S.C. 703-711). The MBTA makes it unlawful to take, possess, buy, sell, purchase, or barter any migratory bird listed in 50 C.F.R. Part 10, including feathers or other parts, nests, eggs, or products, except as allowed by implementing regulations (50 C.F.R. 21). Sections 3503, 3503.5, and 3800 of the California Department of Fish and Game Code prohibit the take, possession, or destruction of birds, their nests or eggs. Implementation of the take provisions requires that project-related disturbance at active nesting territories be reduced or eliminated during critical phases of the nesting cycle (1 March–15 August, annually). Disturbance that causes nest abandonment and/or loss of reproductive effort (e.g., killing or abandonment of eggs or young) or the loss of habitat upon which the birds depend is considered "taking" and is potentially punishable by fines and/or imprisonment. Such taking would also violate federal law protecting migratory birds (e.g., MBTA).

The burrowing owl is a Species of Special Concern to California because of declines of suitable habitat and both localized and statewide population declines. Guidelines for the Implementation of the California Environmental Quality Act (CEQA) provide that a species be considered as endangered or "rare" regardless of appearance on a formal list for the purposes of the CEQA (Guidelines, Section 15380, subsections b and d). The CEQA requires a mandatory findings of significance if impacts to threatened or endangered species are likely to occur (Sections 21001{c}, 21083. Guidelines 15380, 15064, 15065). Avoidance or mitigation must be presented to reduce impacts to less than significant levels.

CEQA and Subdivision Map Act

CEQA Guidelines Section 15065 directs that a mandatory finding of significance is required for projects that have the potential to substantially degrade or reduce the habitat of, or restrict the range of a threatened or endangered species. CEQA *requires* agencies to implement feasible mitigation measures or feasible alternatives identified in EIR's for projects which will otherwise cause significant adverse impacts (Sections 21002, 21081, 21083; Guidelines, sections 15002, subd. (a)(3), 15021, subd. (a)(2), 15091, subd. (a).).

To be legally adequate, mitigation measures must be capable of "avoiding the impact altogether by not taking a certain action or parts of an action"; "minimizing impacts by limiting the degree or magnitude of the action and its implementation"; "rectifying the impact by repairing, rehabilitating or restoring the impacted environment"; "or reducing or eliminating the impact over time by preservation and maintenance operations during the life of the action." (Guidelines, Section 15370).

Section 66474 (e) of the Subdivision Map Act states "a legislative body of a city or county shall deny approval of a tentative map or parcel map for which a tentative map was not required, if it makes any of the following findings:. . .(e) that the design of the subdivision or the proposed improvements are likely to cause substantial environmental damage or substantially and avoidably injure fish and wildlife or their habitat." In recent court cases, the court upheld that Section 66474(e) provides for environmental impact review separate from and independent of the requirements of CEQA (Topanga Assn. for a Scenic Community v. County of Los Angeles, 263 Cal. Rptr. 214 (1989).). The finding in Section 66474 is in addition to the requirements for the preparation of an EIR or Negative Declaration.

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Daniel E. Varland
Special Publications Editor

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DEDICATION

This Raptor Research Report, which focuses its attention on the burrowing owl, is dedicated to Dick and Joan Clark for their tireless and selfless raptor conservation, research, and educational efforts. To them, as our colleagues and friends, we gratefully take this opportunity to say 'thank you'.

J. Raptor Res. Report 9:1

FOREWORD

Although I was never sure that I was the most appropriate person to preface this symposium volume, having been chosen (and therefore sufficiently flattered), it is with great satisfaction that I wish to put in print my impressions about the importance of the work commented henceforth.

This volume is a step forward in providing not only information on burrowing owl biology, but also on its practitioners. Bird-watchers, college and graduate students, academics and professionals will find in a nutshell what has been published in the past about this owl, what is the state of the art, and the addresses of people to contact for further information. This data-filled monograph should be of much utility to anybody wishing to join the ranks of burrowing owl students, and to fellow raptor biologists to learn from and reach out to their previously unknown colleagues in different states and countries.

The subject of the enormous accumulation of knowledge reported in this book is a unique species in several respects. The burrowing owl has a peculiar aspect, biology and distribution. This long-legged creature is generally diurnal, easy to spot due to its preferred open habitats, nests on the ground, and is distributed from Canada to the tip of South America.

The first two features of this owl, diurnality (which is unusual among owls) and use of open habitats, contribute to the enjoyment of amateur bird-watchers, and render it an ideal subject for study by raptor biologists. On the other hand, the third feature mentioned, its nesting on the ground (in the same open and flat areas favored by us humans to develop agriculture and to establish our urban developments), frequently places us in conflict with the burrowing owl. We have the same habitat requirements, and apparently are winning our competitive contest, in both exploitative and interference ways.

Although the burrowing owl is extensively distributed in the Americas, so are we. Cornered, and with no place left to escape, it seems a moral imperative that we humans take care of this little companion during our travel in Spaceship Earth. If this owl cannot renounce to the ecological traits that thousands of years ago made it perfectly fit to live as it chose, then we will have to give up claiming some of its land or otherwise compensate it somehow.

The search for such a compromise demands the concurrence of experts from many fields: anatomy, behavior, conservation, ecology, environmental education, physiology, genetics, reproduction, taxonomy, systematics, wildlife management, etc. It also requires input from many professionals: biologists, veterinarians, rehabilitators, land managers, urban developers, and, indeed, individuals from all walks of life, from students of all grades, to park rangers, politicians, and citizens in general.

Too much to ask? Apparently not. Judging from the variety of contributors to this volume, I see a broad cross-section of disciplines and professionals aiming at understanding the threats and necessities of the burrowing owl and providing some solutions. As long as this situation remains, and more people are incorporated into appreciating the desirability of coexisting with our fellow neighbor, the burrowing owl, there is hope that we may reach a compromise.

There is a final aspect that may facilitate a convergence of wills toward putting up the burrowing owl as an honorable case of meeting our respective demands in the middle. In the same way as the cosmopolitan barn owl may be considered as a raptorial world ambassador, the burrowing owl is an ambassador for the Americas (all three of them, and the Caribbean). They share some behavioral traits with our human ambassadors: they tend to live under the spotlight, travel a lot, and are located in many American nations. Sometimes they are threatened, and, like the burrowing owl, require strong backing from their governments.

The constituency of our ambassador, the burrowing owl, is us—the human beings. I believe that it is in the best of all our interests to provide comfort and support to our owl. I see in this volume that I am prefacing that we are off to a good start. Let's make it to the finish line!

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Ecology Department
Catholic University of Chile

J. Raptor Res. Report 9:2

BACKGROUND

Origins. The conception of the First International Burrowing Owl Symposium (BOS) can be traced back to conversations with Paul James and Joe Schmutz. Each expressed concern over the fate of the burrowing owl (*Speotyto cunicularia*) in their country, Canada, and throughout its range.

Embryonic development of this effort followed discussions with Butch Olendorff, Dick Clark, and Jack Barclay, which confirmed the level of concern and the identification of our BOS Steering Committee. The Steering Committee was made up of eleven individuals from the United States, five from Canada and three from Latin America. Once we agreed that the symposium should take place in conjunction with the Annual Raptor Research Foundation (RRF) Conference in Seattle, we added five ex-officio members, made up of individuals representing RRF and/or coordinating the RRF conference's scientific program.

Hatching started on 13 November 1992 in the form of the symposium. It consisted of eighteen paper presentations and seven posters, and was attended by 130 individuals. On the following day, hatching was consummated with a workshop that addressed the most pressing management and research needs associated with this species. The workshop was a wonderfully serendipitous event, taking advantage of the presence of many of the world's most knowledgeable burrowing owl conservation biologists.

Objectives. The objectives of the symposium and workshop were to: (1) share information; (2) identify the most pressing management and research needs; and (3) take a significant step toward an action plan for this species.

What Follows. A paper on the taxonomy of the burrowing owl sets the stage for our task of understanding this species' needs. Three invited papers follow and give the reader a review of the status of the burrowing owl; an overview of the literature, based primarily on a review of the citations provided in Appendix A; and the results of the above Burrowing Owl Workshop, which followed the symposium.

The next section of this document is the symposium proceedings, *per se,* and includes both updated and expanded oral and poster presentations. These have been divided, somewhat arbitrarily, into population ecology and status, genetics and breeding biology, management, and other issues.

Finally, an attempt was made to provide as comprehensive a list as possible of relevant references (Appendix A). As admitted "bibliophiles" (a term I first heard from Butch Olendorff), we recognize how quickly such lists can become out-of-date. Hopefully, however, this product will become a springboard that will help propel future efforts toward the goal of proper environmental management for the burrowing owl.

Thanks. Thanks go to Paul James, Joe Schmutz and others who encouraged me to move forward on this project, and to all the authors, peer reviewers and the following members of the Steering Committee: Jack Barclay, Isabel Bellocq, Steve Brechtel, Richard Clark,* Mike Collopy,* Ken De Smet, Orville Dyer, Fabian Jaksić, Paul James, Brenda Johnson, Jeffrey L. Lincer, James MacCracken, Kay McKeever, Carl Marti, Brian Millsap, Richard R. Olendorff, John Pierce, Claire Puchy, Joe Schmutz,* Steve K. Sherrod, Mark Stalmaster,* Sergio Tiranti, Lenny Young,* and Brian Walton.

Finally, thanks and hearty acknowledgments go to those who, in a variety of important ways, supported this publication: The Raptor Research Foundation for making it easy to assemble many of the world's most knowledgeable burrowing owl biologists and managers, Sweetwater Environmental Biologists, Inc., The National Biological Service, World Wildlife Canada, The Denver Museum of Natural History, and the state of Florida's Nongame Program for financial assistance; my co-editor, Karen Steenhof, for her much-needed assistance, Joan S. Clark for proofreading skills beyond my comprehension and Sean Klope, for his word processing support; Allen Press for their guidance; and finally, my wife Carolyn for giving up many of "our" evenings and weekends in order that these proceedings see the light of day.

Jeffrey L. Lincer, Chair
Burrowing Owl Symposium

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* Ex-Officio Members.

INVITED PAPERS

J. Raptor Res. Report 9:3–5

CURRENT STATUS OF THE BURROWING OWL IN NORTH AMERICA: AN AGENCY SURVEY

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ABSTRACT.—The current status of the burrowing owl (*Speotyto cunicularia*) in North America (excluding Mexico) was assessed by mailing a questionnaire to the wildlife agencies of the 24 states and provinces in which burrowing owls breed. Each agency was asked to estimate, to the nearest order of magnitude, the size of its breeding population and to indicate whether or not the population was stable, increasing, or decreasing. In addition, each agency was asked to identify limiting factors affecting burrowing owls, and to indicate whether any special status was given to the species. Of the 24 jurisdictions, 11 (46%) reported a population between 1000 and 10 000 pairs, and 8 (33%) reported a population between 100 and 1000 pairs. Thirteen (54%) reported that their owl population was probably declining, and no agency reported an increase. Habitat loss (83% of respondents), reduced burrow availability due to rodent control (54%), and pesticides (46%) were the most important limiting factors identified. Sixteen (67%) of the jurisdictions give burrowing owls special status above that of regular protection.

KEY WORDS: *burrowing owl*; Speotyto cunicularia; *status*; *North America*.

Estado actual del tecolotito enano en Norte America: Encuesta de agencias

RESUMEN.—El estado actual del tecolotito enano (*Athene cunicularia*) en Norte America (excluyendo Mexico) se evaluo por medio de un cuestionario enviado por correo a agencias de fauna silvestre en 24 estados y provincias en las cuales el tecolotito se reproduce. A cada agencia se le pidio estimara, al orden de magnitud mas cercano, el tamaño de su poblacion reproductiva y que indicaran si la poblacion era estable, aumentaba, o disminuia. Ademas a cada agencia se le pidio identificara factores limitantes e indicara si la especie recibia alguna categoria especial. De las 24 juridicciones 11 (46%) reportaron una poblacion entre 1000 y 10 000 parejas y 8 (33%) reportaron una poblacion entre 100 y 1000 parejas. Trece (54%) reportaron que su poblacion de tecolotes estaba disminuyendo y nadie reporto un incremento en sus poblaciones. Perdida del habitat (85% de respondientes), reducido numero de madrigueras debido al control de roedores (54%) y pesticidas (46%) fueron los factores limitantes mas importantes que se identificaron. Diezyseis (67%) de las juridicciones le adjudican categoria especial al tecolotito enano ademas de la proteccion regular.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) is listed as Threatened in Canada (Wedgwood 1978, Haug and Didiuk 1991) and has been on the Blue List (Arbib 1971) in the United States since 1972. Despite this, accurate estimates and trends of burrowing owl numbers remain largely unavailable (Robbins et al. 1986, Root 1988). Analysis of Christmas Bird Counts from 1954–86 have indicated that the wintering population is generally stable, although a decline has taken place since the mid-1970s (James and Ethier 1989). Analysis of Breeding Bird Surveys from 1965–79 has shown only one significant change, an increase in the Glaciated Missouri Plateau Physiographic Region, covering parts of Saskatchewan, Alberta, Montana, North Dakota, and South Dakota (Robbins et al. 1986). Other es-

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Table 1. Results of the 1992 burrowing owl population survey.

JURISDICTION	SIZE[a]	TREND[b]	FACTORS[c]	SPECIAL STATUS
Alberta	low 4	D/S	H, Ps	Yes
Arizona	3	D	H, Ps, B	No
BC	1	D	H, Pr, B	Yes
California	4	D	H, Ps, Pr, Pe, B, V	Yes
Colorado	4	D	H, Ps, B	No
Florida	4	S	H, Pr, V	Yes
Idaho	low 4	S	H	Yes
Iowa	1	D/S	H, B, Ps	Yes
Kansas	3	D	B	No
Manitoba	2	D	Ps, Pr, Pe, V	Yes
Minnesota	1	S	B, V	Yes
Montana	3	S	?	Yes
Nebraska	3	D	H, Ps	No
Nevada	4	D	H, B, Ps	No
New Mexico	4	S	H, Ps	No
North Dakota	3	S	H, B, Ps	No
Oklahoma	3	S	H, B	Yes
Oregon	low 4	S	H, B	Yes
Saskatchewan	low 4	D	H, Ps, F	Yes
South Dakota	3	S	H, B	Yes
Texas	low 5	S	H, B	No
Utah	low 4	D	H	Yes
Washington	3	D	H	Yes
Wyoming	low 4	S	H	Yes

[a] 1 = 1–10 pairs, 2 = 10–100 pairs, 3 = 100–1000 pairs, 4 = 1000–10 000 pairs, 5 = 10 000–100 000 pairs.
[b] D = decreasing, S = stable.
[c] H = habitat loss, Ps = pesticides, B = reduced burrow availability, Pr = predators, Pe = persecution, V = vehicle collisions, F = food availability.

timates of breeding populations are largely nonexistent, so it was decided to conduct a survey of wildlife agencies to determine the current status of this owl in North America.

METHODS

A questionnaire was mailed out to all 24 state and provincial wildlife agencies within the breeding range of the burrowing owl in North America. Four questions were asked in the form of a checklist: (1) What is, to the nearest order of magnitude (1–10 pairs, 10–100 pairs, 100–1000 pairs, etc.), the breeding population of burrowing owls in your jurisdiction?; (2) Is this population stable, increasing, or decreasing?; (3) What limiting factors are important in your breeding population?; (4) Does your jurisdiction provide burrowing owls with any special status? If so, what?

RESULTS

All 24 wildlife agencies responded to the questionnaire (Table 1). Of these, 11 (46%) estimated their burrowing owl population at between 1000 and 10 000 pairs, and 8 (33%) estimated their population at between 100 and 1000 pairs. Only one (Texas) estimated a population of over 10 000 pairs, while the remaining four jurisdictions held between one and 100 pairs. However, despite these relatively healthy estimates of numbers, 13 (54%) reported that their owl population was probably declining, and no one reported an increasing population. Seven potentially limiting factors were identified. Of these, habitat loss (83% of respondents), reduced burrow availability due to rodent control (54%), and pesticides (46%) were the most important. Finally, 16 (67%) of the respondents give their burrowing owls some form of special status over and above that of regular protection.

DISCUSSION

Although the total breeding population of burrowing owls in North America appears to be still relatively healthy, there is concern because over half of the jurisdictions reported declining populations (Table 1), and no one reported an increasing population. This is somewhat consistent with recent Christmas Bird Count analyses (James and Ethier 1989), but at odds with Breeding Bird Survey results for the period 1954–1986 (Robbins et al. 1986).

Factors such as habitat loss, reduced burrow availability, and pesticides were cited as important. Although studies of habitat selection by burrowing owls have been conducted (Rich 1986, Green and Anthony 1989, James et al. 1991), recent rates of conversion of grassland to cropland or urban development have rarely been reported. In Saskatchewan, e.g., between 1979 and 1986, 21% of the remaining grassland habitat was cultivated (Hjertaas and Lyon 1987). Clearly, more work is needed to determine recent and ongoing rates of conversion of burrowing owl habitat.

Some studies have also addressed the problem of reduced burrow availability (Hjertaas and Lyon 1987, Green and Anthony 1989, James et al. 1991). Although the use of strychnine for rodent control appears not to directly threaten burrowing owls (James et al. 1990), long-term removal of rodents will likely limit the availability of suitable burrows. This is likely to be particularly true with the already widespread but ongoing removal of prairie dogs (*Cynomys* spp.) in the United States (Miller et al. 1994). Studies on the direct impact of other pesticides are limited (James and Fox 1987, Fox et al.

1989, Fox and James 1991) and have shown that the use of carbofuran is detrimental to burrowing owls. More work is needed, however, on many other pesticides currently registered for use in the agricultural landscapes where burrowing owls often occur.

In summary, the burrowing owl in North America still appears to be quite numerous at present. However, it should be remembered that these data are derived from a questionnaire and few agencies have accurate counts. There is a great need for systematic surveys to be developed and conducted, particularly as over half of the agencies reported declining populations. More research is also needed on potentially limiting factors, and attention needs to be focused on agricultural policies throughout western North America that promote the destruction of native grassland habitat and its associated burrowing mammals.

ACKNOWLEDGMENTS

We thank all of the wildlife agency staff who took the time to complete the questionnaire. Work on burrowing owls has been supported by the Canadian Wildlife Service, FMC Canada, Nature Saskatchewan, Wildlife Habitat Canada, Wildlife Toxicology Fund, and World Wildlife Fund. B. Millsap, R. Olendorff, and K. Steenhof improved the manuscript. This paper is dedicated to the memory of Joanna Tudan-Sainberg.

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J. Raptor Res. Report 9:6–10

OVERVIEW OF LITERATURE ON THE BURROWING OWL

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ABSTRACT.—We examined titles for each of 845 burrowing owl (*Speotyto cunicularia*) citations included in the extensive bibliography prepared for this volume by R. Clark, J. Lincer, and J. Clark to determine year of publication, geographic locale of work, and topic reported. Although we readily admit that our review of citations is not an optimal approach to understanding the breadth of current knowledge about the burrowing owl, we believe our review provides a broad measure of the extent of work on different populations and facets of the biology of this species. Rate of publication of papers on the burrowing owl has been increasing since the early 1930s, with a rapid increase since the late 1970s. Most articles deal with the burrowing owl in North America (89% of all regional publications), and nearly half of North American papers were based on studies in Washington, California, or Florida. Burrowing owls in Mexico, Central America, South America, and the West Indies are vastly underrepresented in the literature for the species. Not surprisingly, there is a heavy subject bias in the published literature toward burrowing owl life history. There are surprisingly few papers dealing with conservation subjects, especially such topics as livestock grazing, pesticides, and land use impacts—issues that beg attention in today's environment.

KEY WORDS: *literature*; *burrowing owl*; Speotyto cunicularia; *trends*.

Revision de la litertura del tecolotito enano

RESUMEN.—Examinamos titulos de 845 citas del tecolotito enano (*Speotyto cunicularia*) incluidas en la extensa bibliografia preparada para este volumen por R. Clark, J. Lincer y J. Clark con fines de determinar el año de publicacion, localidad del trabajo y tema reportado. Aunque admitimos que nuestra revision de citas no fue de la manera mas optima para entender la variedad del conocimiento actual del tecolotito, creemos que nuestra revision provee una medida amplia de la extension de trabajos en diferentes poblaciones y facetas de la biologia de esta especie. La publicacion de articulos sobre el tecolotito enano ha incrementado desde principios de los años 1930's con rapido incremento desde fines de los años 1970's. La mayoria de los articulos tratan con el tecolotito en Norte America (89% de las publicaciones regionales) y casi la mitad de articulos Norte Americanos se basan en estudios realizados en Washington, California o Florida. El tecolotito enano esta mal representado en la literutura de la especie en Mexico, Centro America, Sud America e Indias Occidentales. Existe un zezgo hacia la literatura publicada sobre los habitos de vida del tecolotito enano. Existen pocos articulos que tratan con temas de conservacion, especialmente tales temas como el pastoreo de ganado, pesticidas, e impactos del uso de la tierra—temas que requieren atencion en el mundo de hoy.

[Traducción de Filepe Chavez-Ramirez]

The purpose of this paper is to present a brief overview of literature published through 1993 on the burrowing owl (*Speotyto cunicularia*). The basis for this summary is the exhaustive bibliography that has been assembled for this volume by R. Clark, J. Lincer, and J. Clark. We classified the references according to year, geographic locality, and subject matter based on information contained in

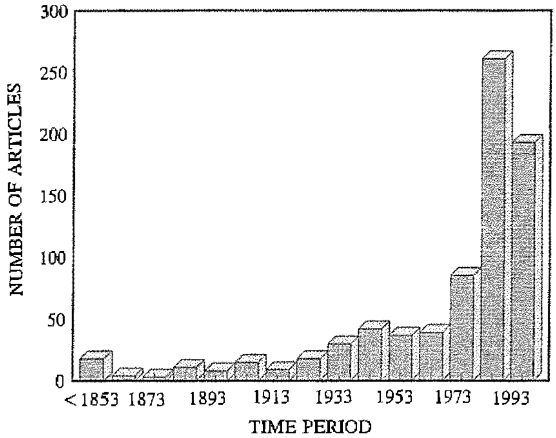

Figure 1. Distribution of burrowing owl publications by year.

the citation. In so doing, we have identified areas (both geographic and topical) that are both strongly and poorly represented in literature for this species.

METHODS

We converted a text file of the bibliography prepared by the above authors into a data base format with fields for author, year of publication, and title. We reviewed each entry and, according to information in the title, classified citations as to: (1) year of publication, (2) geographic area of work, (3) whether the publication was a scientific or popular article, (4) whether the article was specific to burrowing owls or dealt with more than one species, and (5) the major subjects (up to six) covered in the paper. Our analysis consisted of simple counts of citations by decade of publication, geographic area, article type, and subject. There are obvious limitations to this type of analysis, not the least of which is the possibility that the title may not adequately indicate the scope of the work reported. However, with cautious interpretation, we believe our analysis provides a useful overview of the literature for this species.

RESULTS

Temporal Distribution of Literature. As with raptor literature in general (Olendorff et al. 1980), the rate of publication of articles dealing with burrowing owls has increased in recent years (Fig. 1). Whereas the upswing in general raptor publications was not noticeable until the 1950s (Olendorff et al. 1980), the increase for burrowing owl literature began during the early 1930s with a strong second peak beginning in the 1970s. Clark et al. (1987) observed a similar 1930s upswing in the number of publications on nine other species of owls, based on 6590 articles listed in Clark et al. (1978). The slight downward trend in the number of burrowing owl articles in the most recent decade is probably an artifact of incomplete sampling of recent journals, particularly those published in late 1993. The recent emphasis toward more long-term studies might also contribute to this trend.

Geographic Distribution of Literature. Of 845 citations examined, 219 referred to issues different from ecology (e.g., physiology), where the place of the study was considered unimportant, or had no information on where the study was conducted. Nine publications referred to the world population (e.g., general books), and nine involved more than one country in different continents (e.g., comparative studies).

A total of 685 titles was assigned to geographic areas. North America accounted for 613 (89%), South America 41 (6%), Central America (including the West Indies) 23 (3%), and the rest of the world 8 (1%) (Fig. 2). Of the North American countries, 504 (82%) citations referred to burrowing owl populations in the United States, 84 (14%) in Canada, 5 (1%) in Mexico, and 20 (3%) referred to more than one North American country (Fig. 2). In South and Central America, most contributions came from Argentina, West Indies, Peru, and Chile (Fig. 3).

Many burrowing owl publications referenced populations throughout the United States and Canada. From the citations considered here, 373 were specific to a particular state in the United States while 131 referred to either more than one state or the country. Nearly half of the studies in the United States referred to burrowing owls in Washington, California, or Florida (Fig. 4). In Canada, 23 titles referred to the country or involved more than one province. The remainder of articles were nearly equally distributed among Saskatchewan (19 publications), British Columbia (18 publications), Manitoba (14 publications), and Alberta (10 publications).

Topical Distribution of Literature. We determined subject categories for 757 of the 845 literature citations in the bibliography. The 88 citations omitted were written for popular audiences and were too broad in scope to classify meaningfully. Each citation included in this analysis was classified into one or more of five major and 48 specific subject categories (Table 1).

Nearly all articles in the bibliography dealt with one or more aspects of burrowing owl life history.

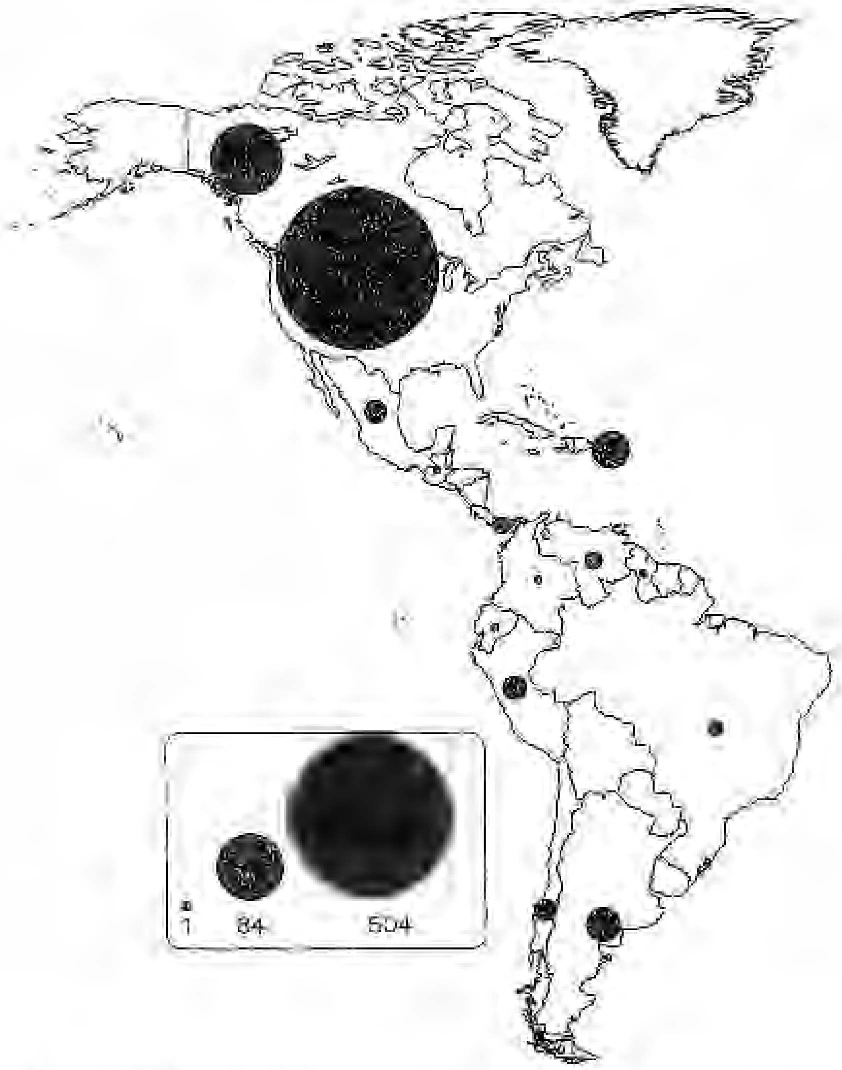

Figure 2. Geographic distribution of burrowing owl work in America. Circles are represented in square root proportion of the number of articles. Countries of the West Indies are represented in one circle for convenience.

The most prevalent topic was distribution, a category that included a large number of records of extralimital or unusual occurrence. General ecology, food habits, broad life history, physiology, and reproduction were other life history topics frequently reported on in the literature. Conservation and management topics comprised the next largest block of subject categories; within this broad area there were no specific categories, except general conservation, that stood out. Population status and technique papers occurred in about equal numbers in the bibliography. We were unable to classify 7% of all citations reviewed to a subject category based on the title.

Discussion

Although our methods were not optimal, we believe our review provides a broad measure of the extent of work on different populations and facets of the biology of the burrowing owl. For example, it is clear that there has been a heavy bias in burrowing owl research toward populations in western

Table 1. Topical distribution of literature for the burrowing owl, based on a review of 774 scientific publications included in the burrowing owl bibliography (this volume).

MAJOR SUBJECT SPECIFIC SUBJECT	NUMBER (%) OF PUBLICATIONS
Conservation/management	117 (15%)
Artificial burrows	5
Artificial perches	2
Broad conservation	46
Disturbance	4
Endangered species	16
Human dimensions	6
Land use	2
Management plans	9
Oil and gas impacts	1
Pesticides	8
Prescribed fire	1
Rehabilitation	6
Reintroduction	6
Relocation	3
Urban wildlife	2
Life history	765 (99%)
Disease	3
Behavior	19
Distribution	349
Ecology	39
Eggs	5
Food habits	67
Habitat	8
Gen. life history	90
Migration	8
Molt	7
Mortality	4
Mutualism	1
Paleontology	8
Parasitism	12
Physiology/anatomy	56
Reproduction	69
Roosting	1
Sexual dimorphism	3
Soils	2
Taxonomy	9
Vocalizations	5
Population status	71 (9%)
Abundance	7
Census	19
Populations	15
Status	30
Techniques	58 (7%)
Banding	6
General	10
Identification	25
Public relations	3
Statistical methods	1
Survey	8
Trapping	5
Unknown	51 (7%)

Table 1. Continued.

North America. Burrowing owl populations in Mexico, the Caribbean Islands, Central America, and South America remain relatively unstudied (Fig. 2). These populations differ from those in western North America in several ways (e.g., their tendency to excavate burrows in the Florida and Caribbean populations [Haug et al. 1993]), and should prove fruitful subjects for additional work. Not surprisingly, there is a heavy subject bias in the published literature toward burrowing owl life history. There are few papers dealing with conservation subjects, especially such topics as livestock grazing, pesticides, and land use impacts. These areas would seem to be worthy of additional emphasis.

Although over 800 articles have been written on the burrowing owl, one might still wonder how much we actually know about the species, and how critical our lack of information is for the conservation of this species. The high and increasing rate

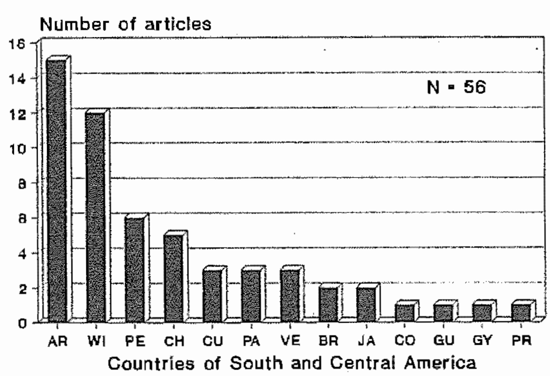

Figure 3. Number of articles on burrowing owl populations in South and Central American countries: AR = Argentina, BR = Brazil, CH = Chile, CO = Colombia, CU = Cuba, EC = Ecuador, GU = Guatemala, GY = Guyana, JA = Jamaica, PA = Panama, PE = Peru, PR = Puerto Rico, VE = Venezuela, WI = West Indies (excluding Cuba, Jamaica, and Puerto Rico).

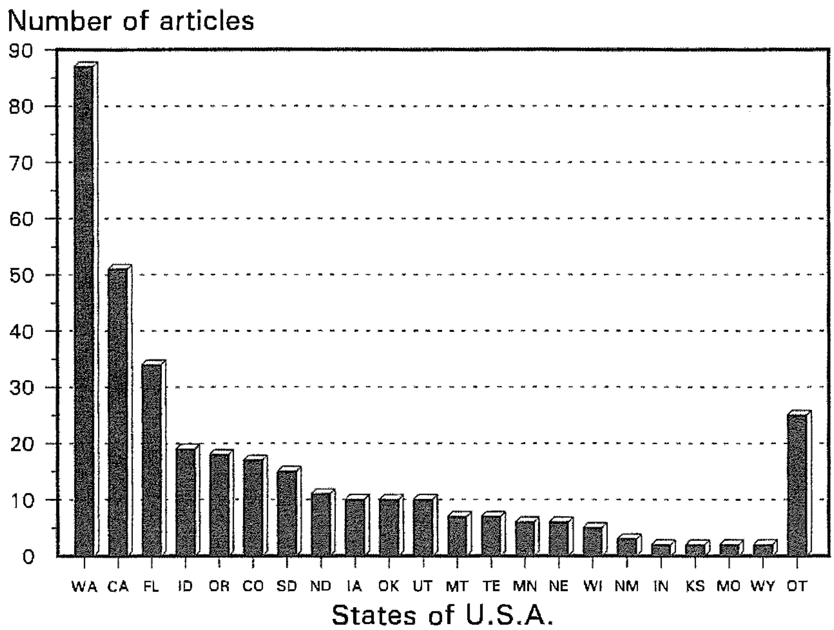

Figure 4. Number of articles on burrowing owl populations in different states in the United States. OT refers to others.

of publication of articles dealing with this species is a positive sign that existing information gaps will continue to narrow.

ACKNOWLEDGMENTS

Our analysis would not have been possible without the painstaking bibliographic work of R. Clark, J. Lincer, and J. Clark; we thank them for sharing their data with us. The manuscript was improved considerably by the reviews of K. Steenhof, R. Clark, and J. Lincer.

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J. Raptor Res. Report 9:11–13

TOWARD AN ACTION PLAN

THE RESULTS OF THE BURROWING OWL WORKSHOP, 14 NOVEMBER 1992, BELLEVUE, WASHINGTON

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ABSTRACT.—A workshop was held after The First International Burrowing Owl (*Speotyto cunicularia*) Symposium and in conjunction with the 1992 Raptor Research Foundation Conference. This workshop had the following goals: (1) identify and prioritize burrowing owl problems and issues; (2) determine if solutions are known; and (3) propose necessary research to address remaining problems and issues. Using the Nominal Group Process and brain-storming committees, approximately 40 biologists and wildlife managers addressed the above goals in a synergistic and productive way.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *issues; problems; solutions; research.*

Hacia un plan de accion, los resultados de un taller sobre el tecolotito enano, noviembre 14 1992, Bellevue, Washington

RESUMEN.—Un taller se realizo despues del Primer Simposio Internacional del Tecolotito Enano (*Speotyto cunicularia*) y en conjunto con la conferencia de 1992 del Raptor Research Foundation. Este taller tuvo las siguientes metas: (1) Identificar y ponerle prioridades a los problemas y situaciones del tecolotito enano; (2) Determinar se se conocen soluciones y; (3) Proponer investigacion necesaria para afrontar problemas y situaciones restantes. Usando el Proceso de Grupo Nominal y comites de discussion, aproximadamente 40 biologos y manejadores de fauna afrontaron las metas propuestas de una manera conjunta y productiva.

[Traducción de Filepe Chavez-Ramirez]

The First International Burrowing Owl (*Speotyto cunicularia*) Symposium was held 15 November 1992, in conjunction with the Annual Raptor Research Foundation Conference in Bellevue, Washington. The symposium drew together scientists and managers from throughout North, Central, and South America. This unique assemblage of some of the world's most knowledgeable burrowing owl biologists afforded the opportunity to discuss and share information relevant to burrowing owl biology, conservation and management. This workshop provided a forum for the definition and discussion of contemporary issues affecting burrowing owls.

GOALS

The goals for this workshop were to identify and prioritize burrowing owl problems and issues; determine if solutions to the above are known; and to propose the research necessary to address those problems for which solutions are not apparent.

METHODS

After a brief review of the previous day's Burrowing Owl Symposium by Brian Millsap and M. Isabel Bellocq, the group was introduced to the Nominal Group Process (NGP). This is a structured process developed by the Rand Corporation to maximize and rank input from a group of knowledgeable participants.

The steps to address the first goal (i.e., identifying problems and issues) involved the standard NGP approach: (1) a silent generation of ideas by each participant; (2) a listing of cumulative ideas by all participants; (3) a discussion of these ideas (for clarification only); and (4) ranking ideas by giving each participant four votes to be distributed over all proposed ideas. The final "rank" is the sum of participant votes assigned to each of the issues and needs.

The remaining goals (i.e., identifying known solutions and necessary research) were assigned to two brainstorming committees which were chaired by Jack Barclay and Robert Lehman, respectively.

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RESULTS

Issues and Needs. The group identified the following issues and needs, during the NGP, as important to the conservation and management of the burrowing owl. These have been ranked from highest to lowest priority by the workshop participants. Minor changes for clarification, and consolidation of similar issues, have been made by the author.

1. General Population Decline Throughout Entire Range.
2. Habitat Loss and Degradation (emphasis placed on total needs, including discing for fire, land use activities, and habitat conversion) Leading to Population Fragmentation and Associated Genetic Problems.
3. Identifying Wintering Areas/Understanding Wintering Ecology/Establishing International Agreements.
4. Decline of Burrowing Mammals (discussion focused on government-sponsored animal damage control programs)/Need for Better Understanding and Management of Prairie Dog and Badger.
5. Public Education, Including Education of Land Managers and Policy-Makers/Encouraging Private Landowner and Public Participation in Protecting Habitat/ Recognizing the Problems of Overloading Demands on Landowners.
6. Prioritizing Issues (include elevated level of strategy, role of biologist, and ecosystem management).
7. High Adult Mortality/Mortality (especially of young) by Vehicles/Mortality of Females and Chicks (from development and associated earth moving).
8. Lack of Standardized Survey Protocols, Reproductive Data, Population Status and Information on Specific Causes of Decline.
9. Effects of Agricultural Chemicals and Other Toxics.
10. Government Policy that Rewards Destruction of Habitat, Lack of National/ Federal, State and Local Regulatory Mechanisms (for native and disturbed habitat).
11. Lack of Behavioral Information, Including Foraging Strategies, Range, Dispersal of Young and Effectiveness of Translocation and/or Relocation.

Known Solutions. The focus of the Solutions Committee was to identify approaches that have already proven productive in the wildlife/people management arena. This group concluded that there were four subject areas into which their findings could be divided: (1) protection of habitat; (2) management of habitat; (3) standardization of survey methods; and (4) reduction of mortality.

This committee emphasized that protection of habitat should include protection of breeding, wintering, foraging, and migration habitats. Mechanisms to accomplish the above protection include: developing and enforcing sound legislative/governmental policy at all levels, including statutes, ordinances, laws, subsidies, and treaties; educating the public to support the above policies; enlisting participation from public and private landowners; and acquiring/protecting priority habitat through fee simple, conservation easement, transfer of development rights or other mechanisms.

Discussions on management of habitat emphasized that management should occur at all levels, from the backyard to the community and ecosystem. Successful mechanisms to manage habitat include: providing education that addresses key habitat components (i.e., burrowing mammals, vegetation, and human activities/land use). In connection with this, the committee created a resolution for the protection of burrowing mammals, which was submitted to, and passed by, the RRF membership for approval (see *Journal of Raptor Research* 27(1):52); and providing financial incentives which would result in avoiding or minimizing the impact of land use on the burrowing owl. For instance, user fees could be charged as a disincentive to a land use which would impact burrowing owl biology. Conversely, incentives could be in the form of a payment to a landowner for not disrupting burrowing owl habitat. An extension of this concept would be payments to a landowner to encourage the protection or establishment of suitable habitats.

Standardized survey methods are critical to assessing the status of a species across its range. Without proper survey protocol and mitigation guidelines, cumulative impacts go unnoticed and opportunities for meaningful mitigation are lost. To address this need, a group called the California Burrowing Owl Consortium recently prepared the "Burrowing Owl Survey Protocol and Mitigation Guidelines." This document is included in these proceedings as Appendix C. These useful suggestions are provided for review and comment but they have not as yet been given any official status.

Mortality can be reduced at several levels, but the following were identified as important mortality factors that should be addressed in any way reasonable: automobile collisions, toxic substances and exogenous organisms (e.g., red foxes (*Vulpes vulpes*) and feral dogs and cats).

Necessary Research. The Research Committee logically concluded that two main threats or proximate factors contribute to population declines—fecundity problems and mortality factors. In part, these threats/factors occur: (1) due to habitat modification or loss within both breeding and wintering ranges (and associated effects on vegetation and prey and burrow availability); (2) during movements (dispersal and migration); and (3) because of genetics (isolation and inbreeding suppression).

The committee concluded that the following prioritized research is needed throughout the species' range:

1. Conduct population surveys (counts) to assess the species' current status;
2. Standardize species-specific terms to facilitate communication between researchers (especially terms relating to reproductive biology);
3. Monitor reproductive success;
4. Identify important mortality factors (both seasonally and geographically);
5. Characterize and inventory habitat (include use of gap analysis to identify important habitats that may require protection);
6. Identify migratory and dispersal patterns;
7. Develop research technology (e.g., radiotelemetry) to improve data collection; and
8. Conduct local demographic studies to determine patterns of population increase, decline, and persistence, and relate patterns to genetic and other influences.

CLOSING

The above ideas and recommendations represent the outcome of a synergistic process involving many dedicated wildlife biologists and environmental managers. The listings are not exhaustive and the author encourages the reader to review the individual papers that follow. In many cases, the authors have recommended management techniques and/or necessary research. The results of the First International Burrowing Owl Workshop and the recommendations of the symposium authors should be taken in concert to develop population-, regional-, and range-level action plans.

ACKNOWLEDGMENTS

This work was supported by Sweetwater Environmental Biologists, Inc. and BioSystems Analysis, Inc. I appreciate both Jack Barclay and Robert Lehman chairing the Known Solutions and Necessary Research Committees on the spur of the moment. This manuscript was reviewed by, and benefited from, the comments of Jack Barclay, Robert Lehman, Mike Collopy, Brian Millsap and Karen Steenhof. I am particularly indebted to the workshop participants: Wendy Aeschliman, Ursula Banasch, Jack Barclay, Sean Barry, David Beig, M. Isabel Bellocq, Janis Buchanan, Gene Butellio, Rebecca Cull, Trish Cutler, Penelope Delevoryas, Dave DeSante, Fred Dobler, Leora Feeney, Lisa Fitzner, Denis Flath, Greg Green, Jerry Hickman, Dale Hjertaas, Geoff Holroyd, Brenda Johnson, Shirley Kendall, Robert Lehman, Jeffrey L. Lincer, Mike Mackintosh, Mark Martell, Carl Marti, Kay McKeever, Brian Mealey, Brian Millsap, Joan Priest, Claire Puchy, Eric Ruhlen, John Schladweiler, Joe Schmutz, Karen Steenhof, Lynne Trulio, Sigrid Ueblacker, Roger Wallace, Troy Wellicome.

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A REVIEW OF THE TAXONOMY AND DISTRIBUTION OF THE BURROWING OWL (*SPEOTYTO CUNICULARIA*)

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ABSTRACT.—The burrowing owl, traditionally, has been widely distributed in both the temperate and tropical xeric grasslands and shrub communities of the Western Hemisphere. Within the Caribbean region at least two of its geographic races have become extinct within historic times. This article summarizes the available information on the anatomical measurements and notes the generally larger size of individuals of continental populations versus island populations. Distributions with regard to the species are presented by geographic races. Areas where the populations are declining are noted; e.g., southern British Columbia, Alberta, Saskatchewan, and Manitoba and regions of California. Uniquely, the race *floridana* of the state of Florida and the Bahama Islands is expanding or recolonizing areas formerly inhabited, at least in Florida.

KEY WORDS: Athene cunicularia; *burrowing owl;* Speotyto cunicularia; *taxonomy; distribution.*

Una reseña de la taxonomía y distribución del Speotyto cunicularia

RESUMEN.—Tradicionalmente, el Búho Madriguero ha estado localizado tanto en las zonas templadas y tropicales como en las comunidades con arbustos dentro del Hemisferion Occidental. Por lo menos dos de sus razas geográficas se han extinguido a través del tiempo dentro de la región del Caribe. Este documento sintetiza la información disponible con respecto a las medidas anatómicas e indica la diversidad de tamaños individualtes en las poblaciones continentales contra las poblaciones de las islas. La distribución de las especies son presentadas de acuerdo a las razas geográficas. Areas donde las poblaciones han declinado, son: al Sur de British Columbia, Alberta, Saskatchewan, Manitoba y las regiones de California. La raza *floridiana* de la Florida y de las Islas del Bahamas, especialmente se ha expandido o ubicado en áreas anteriormente deshabitadas en la Florida.

[Traducción de Filepe Chavez-Ramirez]

Researchers have suggested, among other taxonomic relationships, that the burrowing owl is most appropriately classified within the monotypic Genus *Speotyto* or that it is a long-legged species of *Athene.*

The burrowing owl is widely distributed within grasslands, low-growth shrub, and deserts in the Western Hemisphere. Formerly distributed from the prairie provinces of western Canada to Tierra del Fuego, it has been retreating from both the northern and southern extremes of its range. It has been extirpated from the southern tip of its range and some of the islands of the Carribbean Sea where suitable habitats formerly existed.

METHODS

The material for this review was collected in conjunction with preparations for the production of a revised edition of Clark et al. (1978) working bibliography of owls of the world. Specimens were examined in the museums of Kansas University in Lawrence, the Peabody Museum at Yale University, Louisiana State University in Baton Rouge and the Field Museum in Chicago. Libraries associated with those museums were also checked for appropriate literature. Literature was also acquired for the compilation of a bibliography on the burrowing owl that appears elsewhere in this publication.

TAXONOMY

The burrowing owl was originally ascribed to the Genus *Strix* by Molina (1782) being named *Strix cunicularia.* It underwent a number of name changes (see Strickland [1855], Ridgway [1914] and Peters [1940] for synonyms) until Gloger (1842) placed it in the monotypic genus *Speotyto* in which it remained until moved into *Athene.* Meinertzhagen (1951) had suggested that, based on both anatomical and behavioral characteristics, *cunicularia* be included with *Athene.* He pointed out that *Athene brama* and *Athene noctua,* like *Athene cunicularia,* are "known to breed underground, sometimes in association with snakes and rodents." He also noted that he had observed both *A. brama* and *A. noctua* "excavating with vigour in earth." He further noted that in both genera the nostrils are swollen in a fresh state but the nostril aperture is slightly differently placed in the burrowing owl than in the other two species of *Athene*. Other suggested differences were less tarsal feathering in the burrowing owl with hairs extending to the ends of the toes but lacking on the back of the tarsus. He noted that in some races of *Athene noctua* the hairs may be exactly as in the burrowing owl but that the back of the tarsus is always feathered in that species. Meinertzhagen (1951) also pointed out that the fifth primary in *Athene* is usually distinctly notched but sometimes scarcely perceptible and in the burrowing owl the notching on the outer web of the fifth primary is absent but sometimes slightly suggested. While Sibley and Monroe (1990) stated that "DNA-DNA hybridization evidence indicates that this species [i.e., *Speotyto cunicularia*] is not closely related to *Athene*," Sibley (pers. comm.) acknowledged that in their work they "were not trying to resolve the precise pattern of branching among species within a group" but were rather looking at the older branches on the evolutionary tree. Schmutz and Moker (1991) state, based on cytogenetic evidence, that the "former distinct status [i.e., of being a monotypic Genus *Speotyto*] may be more appropriate." They suggest that the burrowing owl karyotype may be a relatively primitive species with characteristics having closer affinity to an ancestral owl species than that of the other species of *Athene*. Olson and Hilgartner (1982) indicated that *Speotyto* has been separated from *Athene* based on the "greatly lengthened tarsometatarsus, correlated with the highly terrestrial and fossorial habits of the bird." In additon, they pointed out that in the absence of other osteological differences it was better to emphasize the similarities rather than the differences by including *cunicularia* with *Athene*. Ford (1966) recommended inclusion of *cunicularia* within *Athene* based on osteological considerations. Scherzinger (1988) has made a strong case for "cancellation of the genus *Speotyto* and the assimilation of the burrowing owl in the genus *Athene*" basing his recommendation on careful comparisons of vocalizations.

Speotyto cunicularia is widely distributed where there are stretches of open land in arid and semiarid climates but also in wetter climates. Ford (1966) reported fossil remains of an extinct species

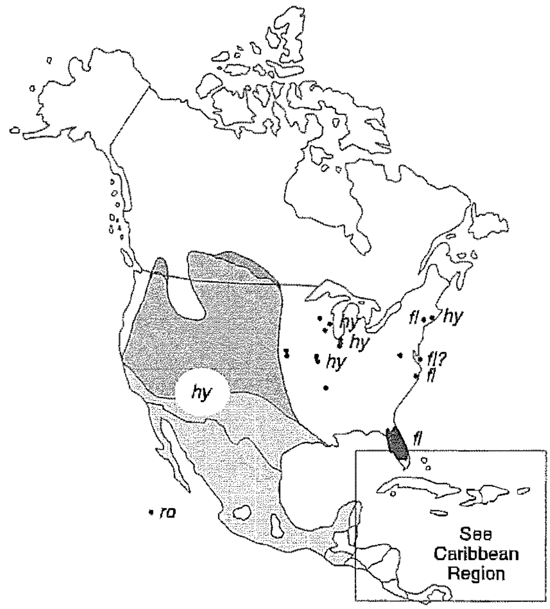

Figure 1. Distributional range of the races *hypugaea* (hy), *floridana* (fl) and the island race *rostrata* (ro). Dark shading at the northern limits of *hypugaea* indicates areas of declining numbers. The next lighter shading is the breeding range from where most birds would be expected to migrate for the winter period, south of which they are permanent residents (lightest shade).

of owl *Speotyto megalopeza* "which appears to have been very similar to the modern *Speotyto cunicularia*, differing most notably in being more robustly built," from Upper Pliocene deposits in Meade County, Kansas. Ford and Murray (1967) reported a fossil of *Speotyto megalopeza* from Upper Pliocene (3.48 ± 0.27 million years B.P.) that came from Twin Falls County, Idaho. Voous and Cameron (1988) speculate that the Old World little owl (*Athene noctua*) is an early descendant and colonist from North America, perhaps in early post-Tertiary times. Lundelius et al. (1983) indicate *Speotyto cunicularia* from archeological sites in California and New Mexico from the Late Pleistocene and Steadman et al. (1984) recorded fossils of it from the time period 4300 to 2500 yr B.P. from Antigua (Lesser Antilles) and indicated they were of the recently extinct race *amaura* (last collected in 1890, Cory 1891). Olson and Hilgartner (1982) noted fossil remains of the burrowing owl from Jamaica, Barbuda, Mona and Cayman Brac, four islands where it no longer exists. Geographic races are listed below chronologically; i.e., according to the

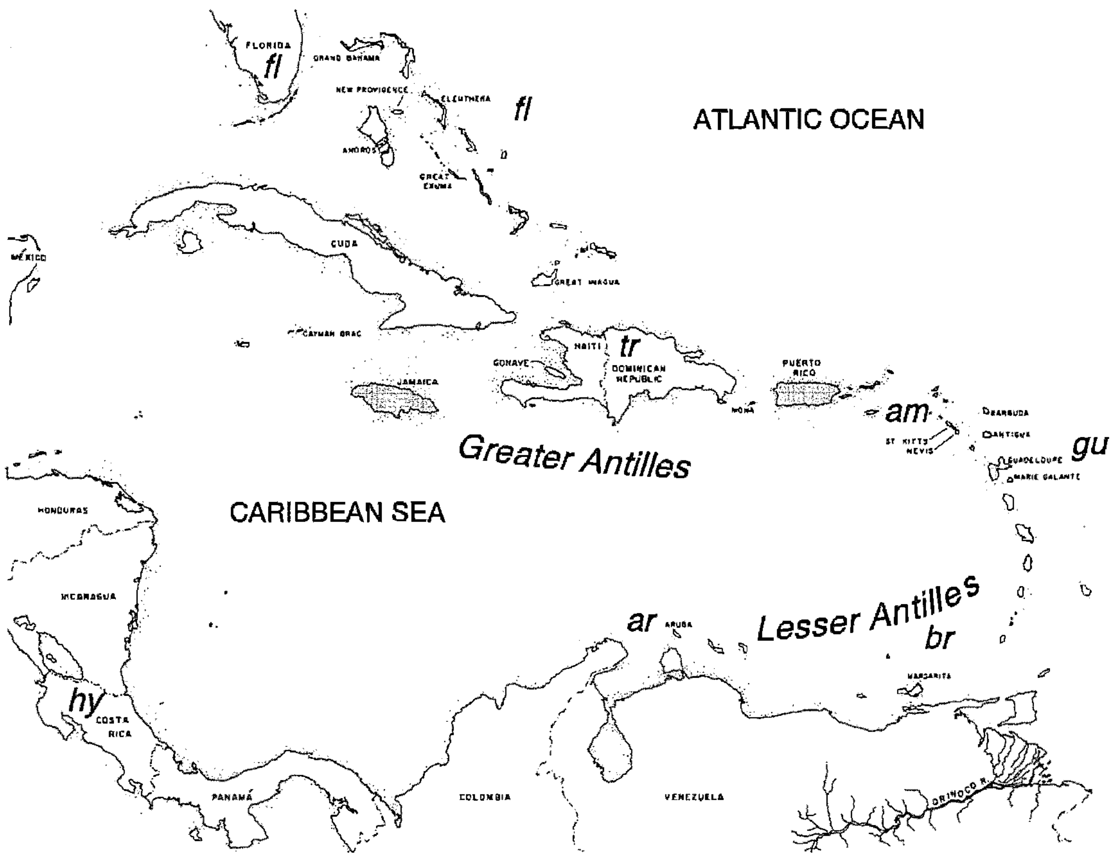

Figure 2. Distributional (or former) ranges of the races *troglodytes* (tr), *amaura* (am) extinct, *guadeloupensis* (gu) extinct, *brachyptera* (br) (this race is known to exist on mainland Venezuela) and *arubensis* (ar) (known only from Aruba Island). All islands named have had or presently have populations of the burrowing owl except they are known to no longer exist on Cayman Brac, Jamaica, Mona, Puerto Rico, Barbuda, St. Kitts, Nevis, Antigua, Guadeloupe, and Marie-Galante. Shading indicates those islands where it has been extirpated or become extinct. Researchers/observers of the other islands should watch carefully for their presence.

date of original description. Their approximate geographic distributions are shown in Figs. 1, 2 and 3 and include the following:

cunicularia (Molina 1782)—Chile from Tarapacá to Cautín; southern Bolivia; Paraguay; Uruguay; southern Brazil in State of Rio Grande do Sul; Argentina south to Tierra del Fuego. In Chile, along the coasts and the sparsely vegetated hillsides of the Andean foothills up to about 1524 m (5000 feet), from Tarapacá south to Valdivia (Johnson 1967). Throughout Argentina from the plains and foothills of Patagonia to the Chaco and pre-puna of the northwest where Olrog (1976) described the race *partridgei*. It is likely extirpated from Tierra del Fuego since the early 1920s (Humphrey et al. 1970). It was probably common in the northern, nonforested portion of the island and its disappearance coincided with widespread sheep-grazing and may have resulted from sheep trampling the burrows.

grallaria (Temminck 1822)—dry interior of Brazil from Maranhão and Piauhy southward through Goyaz and Bahia to southeastern Matto Grosso and Paraná.

hypugaea (Bonaparte 1825)—southern British Columbia east to central Manitoba, south along the eastern edge of the Great Plains, and south to western Panama. James (1992) presented strong evidence that Canadian birds winter at least as far south as Central America and James and

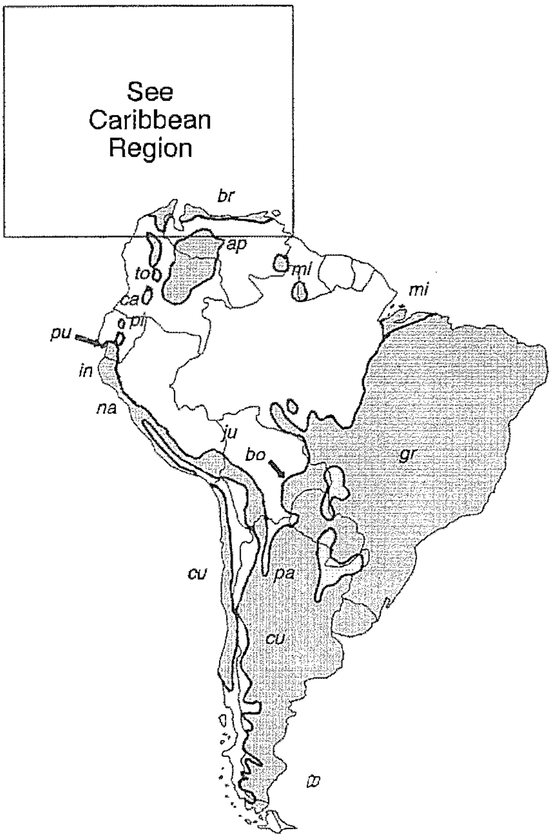

Figure 3. Distributional range of the races *apurensis* (ap), *boliviana* (bo), *brachyptera* (br), *carrikeri* (ca), *cunicularia* (cu), *grallaria* (gr), *intermedia* (in), *juninensis* (ju), *minor* (mi), *nanodes* (na), *partridgei* (pa), *pichinchae* (pi), *punensis* (pu), and *tolimae* (to). Much work is needed on the distributional range of many of these races and birds from areas of intergrading should be examined very carefully. Much information is needed from the field for most all races.

Ethier (1989) showed that their numbers have been declining steadily since the mid 1970s. Land (1970) suggested that "most, possibly all, Central American records seem to be of migrants from the north." Wetmore (1968) indicated that "stragglers reach western Costa Rica, and there is one record in Panamá . . . at Divalá, Chiriquí." Specimens found outside of the normal range, having been collected or seen and positively identified to be of this race are shown in Figure 1 and were from Wisconsin (Pelzer 1942, Wilde and Oar 1981), Illinois (Musselman 1931), Indiana (Hine 1924, Kirkpatrick 1942), New York (Bull [1974] stated that the individual, which was collected on Long Island, "may well have wandered from the west, but definite proof is lacking"–indicating that it may have been an escaped captive bird; Davis 1977, Richard 1988), Missouri (Easterla 1967), and Virginia (Duncan 1922, Lewis 1988). It should be noted that the determination of this last-mentioned bird, in Virginia, was based on the bird being "very pale compared to any illustrations of the Florida phase" that the author had seen and the "rather small bill, whereas the Florida phase is described as having a large bill for its size." Table 1 shows the *floridana* race as having a culmen about 2 mm longer than that of the western race *hypugaea* and the aforementioned author did not indicate that the bird was ever in the hand. The pattern of *floridana* birds along the Atlantic coast (see below) suggests that perhaps the birds might be "hitchhikers" on ships.

floridana (Ridgway 1874)—the prairies of central and southern Florida, Bahama Islands. Bond (1943) reports that he received notification of a bird of this race being taken at Campo Florido, Havana, Cuba. Barbour (1943) reported that he tried to collect two birds at the western tip of Grand Bahama and they "flew directly out to sea in the direction of Florida." A "careful search of several days duration . . . finally convinced me that these birds had probably shot right across to the mainland" (Barbour 1943). Betz (1932) reported it breeding on Hog Island off the west coast of Pinellas Co., Florida during 1929 through 1932. Neill (1954) reported the northward expansion of this race (to Ocala). Ligon (1963) reported it had continued to Gainesville and Chiefland and south into the Florida Keys (Marathon Key). Sprunt (1938) had reported a number of birds seen along the highway from Tavernier to Marathon (Lower Matecumbe Key, Long Key, Grassy Key and Key Vaca). Ligon (1963) pointed out that as fossil records of the species are recorded from Alachua and Marion Counties they are actually recolonizing former (prehistoric) range. Courser (1979) reported that they had been recorded breeding further north in Lafayette, Duval and Suwannee Counties. This recent range expansion has apparently been in response to large-scale clearing of forest for urban development and Millsap and Bear's (1990) reporting of double-brooding by this race indicates favorable breeding conditions. Pub-

Table 1. Anatomical measurements[a] of some burrowing owl races from museum skins (from Ridgway 1914 and Stone 1922).

Geographic Race	Sex	Sample Size	Length (Skins)	Wing	Tail	Culmen	Tarsus	Middle Toe
cunicularia	♂	5	[b]	179.5	86.6	16	47.3	21.7
	♀	5		181	83.7	15.5	46.8	21.7
hypugaea	♂	26	224 (200–245)	172.3 (164.5–178)	81.6 (74.5–86)	14.2 (13–15)	45.3 (41.5–48.5)	20.3 (19–22)
	♀	33	223 (205–250)	170.3 (162.5–181)	79 (71.5–85.5)	13.9 (13–15)	43 (40–46.5)	19.5 (18–20.5)
rostrata	♂	10	221 (215–235)	165 (160–169)	76.3 (72–79.5)	16.1 (15.51–17)	47.1 (45.5–49)	21.4 (20–22.5)
	♀	2	198.5 (195–202)	164.2 (164–164.5)	70.2 (70–70.5)	16 (15.5–16.5)	45.2 (44.5–46)	20.7 (20.5–21)
floridana	♂	10	216 (195–230)	164.2 (154.5–170)	76.4 (73–80.5)	14.9 (14.5–15.5)	44.1 (42–46.5)	20.6 (18.5–21.5)
	♀	10	216 (191–235)	163.9 (156–169)	75.6 (70–78.5)	14.8 (14–15.5)	43 (41–45.5)	20.8 (19.5–22)
troglodytes[c]	♂	6	211 (200–230)	157.2 (153–161.5)	73.9 (72–76)	15.2 (14.5–15.5)	42 (38–45.5)	20.5 (19–21.5)
	♀	6	202 (185–210)	157 (145–165.5)	70.3 (64.5–76.5)	14.8 (14–15.5)	41.2 (38.5–45)	20.4 (18.5–21.5)
brachyptera	♂	1	[b]	142	63.5	13.5	40	19
	♀	1		152	63.5	14.5	41.5	18
amaura	♂	3	211 (200–227)	150.7 (145.5–154)	73.3 (70.5–75.5)	14.2 (14–14.5)	40.8 (39.5–41.5)	20.5 (20–21)
	♀	3	249 (218–295)	150 (148.5–151)	72 (70–73.5)	14.8 (14.5–15.5)	39.8 (39.5–40.5)	20.8 (19.5–21.5)
guadeloupe	?	3	"about" 215	160 (158–162.5)	79.5 (75.5–86.4)	15.2 (15–15.5)	44.2 (42.5–46.2)	21.5
carrikeri[d]	?	1	[b]	173	78	14	46	

[a] All measurements in mm.
[b] Data not available from article.
[c] Listed by Ridgway as *S. f. dominicensis* also his text and tabled values do not agree. Text values used.
[d] Stone (1922).

lished records for this race in eastern United States north of Florida include a bird collected at Salvo, Dare County, North Carolina (Sykes 1974), a specimen (presumably of this race) taken just off the coast of Virginia outside of Hampton Roads (Strong 1922) and a bird, identified while in hand, was frequenting an area of Cedar Beach, Suffolk County, New York (Davis 1977). Sykes (1974) pointed out that the bird reported by Strong (1922), and a bird reported as boarding a sport-fishing boat 40 km off the east coast of Florida (Cocoa Beach, Brevard County, Florida) suggest that these northern sightings of *floridana* may be of birds that have moved to those areas, which are all coastal, by hitchhiking on boats. Sykes (1974) notes that "on the southeast coast of Florida the busy coastal shipping lane is within 1–2 km of shore."

guadeloupensis (Ridgway 1874)—Reported as formerly occurring either on the Island of Guadeloupe or Marie Galante in the Lesser Antilles (Peters 1940) and, while Bangs (1930) reported that "this bird really never occurred in Guadeloupe" so the original specimen must have been "from Marie Galante, a drier more arid isle nearby, where the species formerly occurred," a specimen in the Field Museum in Chicago (FMNH catalog number 40487) has listed as the locale of origin "Guadeloupe, West Indies." Extinct. Greenway (1967) indicates its former range as Marie Galante Island, West Indies.

amaura (Lawrence 1878)—Antigua, Nevis and St.

Figure 4. Two birds of the race *troglodytes* in the Louisiana State University (Baton Rouge) museum are interesting in that they show considerable difference in color. The gray bird (left) was a female (collection No. 6567) collected at about 610 m (2000 feet), 12 km northeast of Jarabacoa (Dominican Republic) on 31 October 1963. The rufous bird (right) (collection No. 7934) is a male collected in the same locale as the female on 17 July 1968.

Kitts (Pregill et al. 1988). Extinct. Danforth (1934) noted that this owl was said to have become extinct soon after the introduction of the mongoose.

troglodytes (Wetmore and Swales 1886)—Island of Hispaniola; Beata and Gonave Islands. Two birds of this race (see Fig. 4) in the Louisiana State University museum (Baton Rouge) are interesting in that they show considerable difference in color, a characteristic which is included in some racial descriptions. A gray bird was a female (collection No. 6567) collected at about 610 m (2000 feet), 12 km northeast of Jarabacoa (Dominican Republic) on 31 October 1963. A rufous bird (collection No. 7934) must have been collected in the same locale as the information on the label reads essentially the same except that it is a male collected on 17 July 1968. Does it indicate polymorphism or is one of the birds colored by the soils that it lived in (König pers. comm.)?

rostrata (C.H. Townsend 1890)—Isla Clarión (Clarion Island) off the west coast of Mexico.

nanodes (Berlepsch and Stolzmann 1892)—Chacalluta (Arica) in extreme northern Chile along the coasts and lower-lying valleys north to Trujillo, Peru (Fjeldså and Krabbe 1990, Johnson 1967).

brachyptera (Richmond 1896)—Margarita Island off north coast of Venezuela and parts of mainland. Kelso (1934) listed this as the short-winged burrowing owl, which is, of course, a redundancy, with its racial designation. The data in Table 1 support that designation.

tolimae (Stone 1899)—western Columbia.

juninensis (Berlepsch and Stolzmann 1902)—The puna of the Andes from Jujuy in northwestern Argentina through southwestern Bolivia (Lake Poopó) to the departments of Junín and Lima in central Peru (Fjeldså and Krabbe 1990, Johnson 1967). Koepcke (1970) listed the smaller *nanodes* on the Peruvian coast and low Andean slopes and this larger race in the puna.

Table 2. Distribution of former and present insular races of the burrowing owl.

ISLAND GROUP/ISLAND-LOCALE	RACE	SOURCE	EVIDENCE
Bahamas			
Grand Bahama	*floridana*	Barbour (1943)	live birds
Great Abaco	*floridana*	Olson & Hilgartner (1982)	fossil
New Providence	*floridana*	(Ridgway 1914, Olson & Hilgartner 1982)	skins
Andros	*floridana*	Ridgway (1914)	skins
Eleuthera	*floridana*	(Ridgway 1914, Olson & Hilgartner 1982)	fossil
Little Exuma	*floridana*	(Ridgway 1914, Olson & Hilgartner 1982)	bones
Great Exuma	*floridana*	(Bangs 1930, Olson & Hilgartner 1982)	skins
Crooked Island	*floridana*	(Ridgway 1914, Olson & Hilgartner 1982)	skins
Great Inagua	*floridana*	(Ridgway 1914, Olson & Hilgartner 1982)	skins
Samana Cay	*floridana*	(Ridgway 1914, Olson & Hilgartner 1982)	skins
Cay Sal	*floridana*	Ridgway (1914)	skins
Greater Antilles			
Cuba—Pinar del Río	*floridana*	Olson & Hilgartner (1982)	live birds
—Metanzas	*floridana*?	Olson & Hilgartner (1982)	fossil
—near Guantánamo	*floridana*[a]?	Olson & Hilgartner (1982)	fossil
—Cayos Coco	*floridana*?	Olson & Hilgartner (1982)	
—Guillermo	*floridana*?	Olson & Hilgartner (1982)	fossil
—Daiquirí	*floridana*?	Olson & Hilgartner (1982)	fossil
—Campo Florido, Havana	*floridana*	Bond (1943)	skins
Cayman Brac (extirpated)	*floridana*?	(Olson & Hilgartner 1982, Pregill et al. 1988)	fossil
Jamaica (extirpated)	*floridana*?	(Olson & Hilgartner 1982, Pregill et al. 1988)	fossil
Hispaniola			
Haiti—Le Coup	*troglodytes*[b]	Ridgway (1914)	skins
—Port au Prince	*troglodytes*[b]	Ridgway (1914)	skins
—near Lake Gautier	*troglodytes*[b]	Ridgway (1914)	skins
Dominican Republic—Azua	*troglodytes*[b]	Ridgway (1914)	skins
—between La Vega and Domingo City	*troglodytes*[b]		
—12 km ne of Jarabacoa	*troglodytes*	LSU–Baton Rouge collection	skins
—Gonâve Island	*troglodytes*	Wiley (1986[a])	
—Beata Island		(Olson & Hilgartner 1982, Wiley 1986[a])	fossil
Mona Island (extirpated)		(Olson & Hilgartner 1982, Pregill et al. 1988)	fossil
Puerto Rico	[c]	(Olson & Hilgartner 1982, Wiley 1986[b])	fossil
Lesser Antilles			
Bermuda (extirpated)	*amaura*	(Olson & Hilgartner 1982, Pregill et al. 1988)	fossil
St. Kitts (extinct)	*amaura*	(Wing et al. 1968, Olson & Hilgartner 1982, Pregill et al. 1988)	fossil
Nevis (extinct)	*amaura*		
Antigua (extinct)	*amaura*	(Wing et al. 1968, Olson & Hilgartner 1982, Pregill et al. 1988)	skins
		(Cory 1891, Ridgway 1914, Deignan 1961, Wing et al. 1968, Olson & Hilgartner 1982, Pregill et al. 1988)	skins
Guadeloupe	*guadeloupensis*	Bangs (1930)	skins
Marie-Galante	*guadeloupensis*	(Deignan 1961, AOU 1983)	skins
Redonda	?	Deignan (1961)	skins
Margarita—Porlamar	*brachyptera*	(Deignan 1961, Meyer de Schauensee & Phelps 1978)	skins
La Borracha	*brachyptera*		
Cubagua	*brachyptera*	Meyer de Schauensee & Phelps (1978)	
		Meyer de Schauensee & Phelps (1978)	

Table 2. Continued.

ISLAND GROUP/ISLAND-LOCALE	RACE	SOURCE	EVIDENCE
Revillagigedo group			
Mexico—Pacific Ocean			
Clarion Island	*rostrata*	(Ridgway 1914, Deignan 1961)	skins
Netherlands Antilles			
Aruba	*arubensis*	Cory (1915)	skins

[a] May represent an, as yet, unnamed subspecies (Olson & Hilgartner 1982).
[b] Presumed to be of this race.
[c] Possibly a new species? See Olson & Hilgartner (1982).
[d] When no evidence is offered none is indicated on the table.

punensis (Chapman 1914)—Semiarid valleys of northern Peru to the lowlands of western Ecuador (Fjeldså and Krabbe 1990).
arubensis (Cory 1915)—Aruba Island off northern coast of Venezuela.
intermedia (Cory 1915)—Coast of Peru from south of Payta to Pacasmayo (Peters 1940).
minor (Cory 1918)—Savannas of the upper Rio Branco (Brazil) and probably adjacent parts of British Guiana (Snyder 1966) and Surinam.
carrikeri (Stone 1922)—Known only from type locality (Palmar, Boyaca) in the eastern Andes of Colombia.
pichinchae (Boetticher 1929)—Western Ecuador north to Quito.
boliviana (Kelso 1939)—Arid habitats in tropical Bolivia and northern Argentina.
apurensis (Gilliard 1940)—Northcentral Venezuela.
partridgei (Olrog 1976)—Northwestern Argentina.

DISCUSSION

Although every attempt has been made to include the material from all pertinent literature, much of the distribution of the burrowing owl is within South America and the Caribbean region and the literature is in journals that are not always widely available. It has been the intent of the author to be as inclusive as possible with the literature and to identify those geographic and taxonomic regions where much more work is needed. Olson and Hilgartner (1982) recognized the need to reevaluate the birds from Cuba as there are two races represented there or perhaps a new race. The populations of some of the Caribbean Islands also appear to warrant investigation and one wonders about the possibility of reintroducing the most similar race to those islands where it has been extirpated or where entire races have been eliminated. It is for the convenience of those familiar with those regions or for those who may be traveling to those areas that Table 2 and Figure 2 have been presented. From the anatomical data (Table 1) some trends can be observed; e.g., the continental populations tend to be larger than the insular races. This is particularly true with regard to the tarsal measurements with *rostrata* being something of an exception. It should also be noted that some of the sample sizes are much smaller than desired but, because that is all there is, they are summarized here. While much more information is needed, it should be obtained from live trapped birds, be carefully documented photographically and then the birds should be released back into the wild. Also much needs to be learned about the behavior of the species over much more of its range. It was particularly perplexing trying to work out the distributional range of the various races in South America and it is obvious to me that there is a challenge awaiting some student to assemble the available information from museum specimens. Rocha (1990) could serve as a model for such studies. Also it would be useful to carefully examine, or reexamine in some cases, specimens so that a more accurate picture of the races can emerge. The work that has been and is being done with the species at the limits of its range (e.g., Saskatchewan and Manitoba) and where it is under pressures from anthropogenic development should be extended to the species in the Caribbean and many parts of South America. There seems to be considerable information, with regard to the study of the species, and there seems to be much pertinent information becoming available, or applicable to, the management of the species in areas of high owl-human interaction. Much of this information is available in English but it is needed in Spanish. The inclusion of abstracts and figure and table captions in Spanish, of all articles on the species would be a useful addition where not presently available. Also the careful examination of what is available and the translation of key material into a species management handbook would also seem a useful approach for the conservation of the species. Because of its inhabiting more arid areas, the burrowing owl has been able to stay out of conflict situations in some regions, but as the ever-increasing human population increases its demands for more irrigation-based food, owl-human interaction should be expected to increase in the future and obviously, not in favor of the burrowing owl.

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USING THE AREA OCCUPIED METHOD TO SURVEY FOR BURROWING OWLS IN SOUTH DAKOTA

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Abstract.—Using point-transect survey methods and area occupied analysis we developed a census technique for burrowing owls (*Speotyto cunicularia*) in Badlands National Park, South Dakota. During June and July of 1991, transects were established on four prairie dog towns within the park. We visited stations spaced 300 m apart along the transect for 10 minutes and looked and listened for owls. Surveys were repeated an average of six times on the two towns on which we found owls in 1991, and were also carried out on 11 other towns in the park. Data were analyzed using the area occupied method. We located 12 broods with 29 young, and 31 broods with 99 young in 1991 and 1992, respectively. We estimated the proportion of the area surveyed which was occupied by owls to be 0.34 (SE = 0.07) in 1991 and 0.57 (SE = 0.07) in 1992. The probability of detecting an owl at any occupied station was approximately 0.49. We were able to establish a census technique for Badlands National Park that can be carried out by Park biologists with a minimum of training. Results can be compared among years to form a framework for managing burrowing owls in the Park. We believe that this technique has application to other areas where burrowing owls nest in semi-colonial situations.

Key Words: Speotyto cunicularia; *burrowing owl; South Dakota; survey technique; management.*

Utilizacion del metodo de area ocupada para muestrear tecolotitos enanos en South Dakota

Resumen.—Utilizando los metodos de muetreo de transectos de conteos de punto y area ocupada desarrollamos una tecnica de censar para el tecolotito enano (*Speotyto cunicularia*) en Badland National Park, South Dakota. Durante junio y julio de 1991 transectos se establecieron en 4 colonias de perritos de la pradera dentro del parque. Visitamos estaciones separados por 300 m a lo largo de transectos durante 10 minutos y observamos y escuchamos a tecolotes. Censos se repitieron un promedio de 6 veces en dos colonias en las cuales encontramos tecolotes en 1991 y se llevaron a cabo en otras 11 colonias dentro del parque. Los datos se analizaron usando el metodo de area ocupada. Localizamos 12 nidadas con 29 pollos y 31 nidadas con 99 pollos en 1991 y 1992, respectivamente. Estimamos que la proporcion del area censada que estaba ocupada por los tecolotes era de 0.34 (se = 0.07) en 1991 y 0.57 (se = 0.07) en 1992. La probabilidad de detectar un tecolote en una estacion ocupada era de aproximadamente 0.49. Pudimos establecer una tecnica de muestreo para Badlands National Park que puede realizarse por biologos del parque con un minimo de entrenamiento. Los resultados pueden compararse entre años para formar una base para el manejo del tecolotito enano en el parque. Creemos que esta tecnica tiene aplicacion en otras areas donde los tecolotes anidan en situaciones semi-coloniales.

[Traducción de Filepe Chavez-Ramirez]

Introduction

Accurate survey methods are needed for successful management, research, and conservation of wildlife populations. Many methods have been used to survey raptor populations, including road transect counts, aerial counts, nest searches, and call-playback techniques (Fuller and Mosher 1987). A method to efficiently and accurately survey breeding burrowing owls (*Speotyto cunicularia*) has previously not been available to wildlife managers.

Typically, population data on burrowing owls have fallen into one of three categories: (1) estimates of status at the state or provincial level, usually gathered through questionnaires or "best guesses" (Wedgwood 1976, Martell 1990); (2) searches using call-playback or road transect survey methods (Martell et al. 1990); or (3) in local areas, intensive searches sometimes burrow by burrow, often conducted during the course of a basic research project (MacCracken et al. 1985).

Although intensive searches can lead to finding most owls on a local area, they are time consuming, hard to repeat, and expensive, making them of little use for long-term monitoring or management purposes. Furthermore, burrowing owls are difficult to accurately survey because, like other raptors, they are wide-ranging, secretive, and occur at relatively low densities compared to most game animals (Iverson and Fuller 1989).

This lack of repeatable, economical survey techniques led us to work with the National Park Service to develop a census technique for burrowing owls in Badlands National Park. Our objective was to develop an accurate, repeatable, method for monitoring the Park's burrowing owl population, which in future years could be implemented using Park personnel within the framework of a limited research and management budget.

STUDY AREA

This study was conducted in Badlands National Park which covers 98 865 ha and is located in western South Dakota, approximately 113 km east of Rapid City, SD. It is an area of rugged geological formations including steep "walls" surrounding short-grass plains. These plains consist primarily of western wheatgrass (*Agropyron smithii*), *Bromus* spp., blue grama (*Bouteloua gracilis*), and threadleaf sedge (*Carex filifolia*). Colonies of black-tailed prairie dogs (*Cynomys ludovicianus*) create "towns" covered by buffalo grass (*Buchloe dactyloides*) and needle-and-thread grass (*Stipa comata*) (Agnew et al. 1986), providing ideal habitat for burrowing owls. A herd of nearly 500 American bison (*Bison bison*) also graze the plains in the western portions of the Park.

METHODS

To develop and test the census method, four prairie dog towns (Burns, Tyree I, Roberts, and Sage) with a total area of 760 ha (Table 1) were surveyed six times between 15 June and 15 July 1991. Surveys were repeated on Burns and Tyree I in 1992, but not on Roberts and Sage because of an absence of owls in 1991. Towns were chosen because their size, past management history, and future management plans made them representative of towns in the Park. To obtain an estimate of the Park's burrowing owl population, 13 towns totaling 1506 ha were surveyed at least once in 1992.

We established straight line transects with stations 300 m apart through the prairie dog towns (Ralph and Scott 1981). On smaller towns, transect lines were established through the center of the town. On larger towns, transects were established 300 m apart and parallel to each other allowing for maximum coverage of the area.

Table 1. Burrowing owl brood counts in Badlands National Park 1991–92.

PRAIRIE DOG COLONY	HA.	BROODS 1991	BROODS 1992	JUVENILES 1991	JUVENILES 1992
Burns	204	1	4	2	21
Tyree I	118	5	5	9	16
Tyree II	39	2	1	6	3
Roberts	130	0	1	0	3
Sage	308	0	0	0	0
Kocher I	327	4	9	12	19
Other	380	0	11	0	37
Total	1506	12	31	29	99

The presence of prickly pear cactus (*Opuntia* spp.) and other low-lying vegetation, combined with the owls' cryptic coloration, presented problems in locating owls. Using visual field tests, we determined that a reasonable scanning distance of 150 m from the observation point would allow most Park biologists to reliably locate and identify owls at their burrows.

Each station was visited for 10 min. Using binoculars and 15–60× spotting scopes, we searched for owls within the 150 m radius. In order to maintain consistency and maximize the probability of sighting resident owls, surveys were always done from dawn until approximately 1000 hrs and again from 1900 hrs until 2200 hrs, or until visibility was impaired by darkness. Surveys were not done during inclement weather.

The relatively low densities of owls found on each survey made the use of standard statistical analysis associated with point-transect methods inappropriate. This prompted us to use the "area occupied method" (AO) developed by Geissler and Fuller (1986). Originally developed for censusing diurnal woodland raptors (Iverson and Fuller 1989), the AO technique estimates the proportion of an area which is occupied by a species, thus providing an index of the species abundance.

We also determined the "probability of detecting" (PD) burrowing owls at an "occupied" station. The PD was derived from the repetition of surveys, yielding an arithmatic mean of dl, which is the proportion of detections occurring after the first detection at each stop (Iverson and Fuller 1989). The PD is used as a correction factor for the AO, and can help in future survey design by indicating how many times a transect line should be walked to ensure adequate coverage.

To determine the AO, we recorded whether an adult owl was detected at each station on the transect (i.e., within the 150 m radius). The number of stations on a town that were occupied by adult owls was divided by the total number of stations, then multiplied by the PD correction factor. The resulting statistic gave the proportion of the area which was occupied by owls, along with esti-

Table 2. Probability of detection and area occupied by burrowing owls in Badlands National Park 1991–92.

	Probability of Detection				Area Occupied			
	Mean	SE	95% CI	*N*	Mean	SE	95% CI	*N*
1991	0.448	0.097	0.247–0.663	48	0.340	0.070	0.186–0.499	75
1992	0.564	0.068	0.428–0.700	75	0.570	0.072	0.439–0.723	129
2 yr	0.486	0.056	0.376–0.598	123	—	—	—	

mated SE and 95% Confidence Intervals (CI). Geissler and Fuller (1986) present a detailed explanation of AO and PD along with the equations necessary for computation.

Results

In 1991 we located 12 broods and counted 29 young during our surveys, while in 1992, sampling a much larger area of the Park, we located 31 broods and counted 99 young (Table 1). We estimated that owls occupied 34% (SE = 0.07) of the area occupied by prairie dog towns in the Park in 1991 (N = 75 stations, 95% CI between 0.19–0.5) and 57% (SE = 0.07) of the towns in 1992 (N = 129, 95% CI between 0.44–0.72) (Table 2). In 1991, using data from four prairie dog towns (N = 48 stations), we determined the PD was 0.45 (SE = 0.1), with a 95% CI of 0.247–0.663. When we combined this with the data from Tyree and Burns sites in 1992 (total N = 75 stations), we obtained a PD of 0.486 (SE 0.056) and reduced the 95% CI to 0.376–0.598 (Table 2).

Discussion

We located more owls in the Park in 1992 than in 1991. This is partially due to having increased the area surveyed in 1992 (from 760 to 1506 ha). The increased number of broods on three of six towns in 1992 (Table 1), combined with an increase in the AO from 0.34 to 0.57 (Table 2), indicates a real increase in owl numbers.

The probability of detecting a burrowing owl on our study area was relatively good at 0.49. This compares with an average PD of 0.34 for red-shouldered hawks (*Buteo lineatus*) in Indiana (Iverson and Fuller 1989). Some variation in PD is to be expected with the variations in habitat and owl behavior. However, the PD on individual towns was fairly consistent ranging from 0.33 on Roberts in 1992 (only one station having a sighting) to 0.71 on Tyree in 1992.

We believe that visually counting burrowing owls on a walking point-transect survey is an appropriate census technique for Badlands National Park. It is a relatively simple and inexpensive method which can be carried out in the future by Park biologists with a minimum of training. Using the area occupied method of analysis will allow Park managers to monitor the long-term stability of owl populations and form a framework for future management. Park biologists will also be able to assess the effects on burrowing owls of management actions taken in the Park. This may include such activities as black-footed ferret (*Mustela nigripes*) reintroduction or changes in prairie dog control programs. This technique can be applied to other areas where burrowing owls nest in semicolonial situations, especially where the species is not considered endangered but monitoring is desired. It must be remembered that this technique provides an index, not an actual count, of owls (Iverson and Fuller 1989). Thus, for areas where there are serious concerns about an endangered owl population, more intensive surveys combined with population data are certainly needed.

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DEMOGRAPHY AND POPULATION DYNAMICS OF THE BURROWING OWL

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Abstract.—I used deterministic, age-structured analytic models to examine the demographic causes of projected and observed declines in the size of a color-marked burrowing owl (*Speotyto cunicularia*) population, and to predict its persistence time. Estimates of burrowing owl demographic parameters were calculated from direct observations and from genetic analyses of reproductive success. Comparison of theoretical expectations (based on actual demographic traits) with the real dynamics of the population over ten years showed that the population declined to reproductive extinction in half the time predicted by the models. This discrepancy suggests that stochastic variation in demographic traits, possibly caused by weather, along with stochastic and deterministic changes in genetic structure, also contribute to the dynamics and persistence of burrowing owl populations.

Key Words: *Burrowing owls;* Speotyto cunicularia; *demography; population dynamics; population modeling.*

Demografia y dinamica de poblacion del tecolotito enano

Resumen.—Use modelos deterministicos de estructura de edades para examinar las causas demograficas de disminucion proyectadas y observadas en el tamaño de una pobalcion marcada del tecolotito enano con fines de predecir su tiempo de persistencia. Estimaciones de parametros demograficos del tecolotito se calcularon de observaciones directas y de analisis genetico del exito reproductivo. Comparaciones de expectativas theoricas (en base a rasgos demograficos reales) con la dinamica de la poblacion atravez de 10 años mostro que la poblacion disminuyo a extincion reproductiva en la mitad del tiempo predicho por los modelos. Esta discrepancia sugiere que variaciones fortuitas en rasgos demograficos, posiblemente el clima, ademas de cambios al azar y deterministicos en la estructura genetica tambien contribuyen a la dinamica y persistencia de poblaciones del tecolotito enano.

[Traducción de Filepe Chavez-Ramirez]

The dynamics of populations are collectively governed by demographic traits (such as birth and death rates), population size, degree of spatial subdivision, and levels of immigration and emigration. As natural populations become smaller and more subdivided due to human activities, population ecologists have focused their attention on how variation in demographic parameters, population size, and spatial structure interactively affect population dynamics, and especially the prospects for species extinction or persistence (Gilpin and Soulé 1986, Goodman 1987a,b, Shaffer 1987, Lande 1988, Simberloff 1988). Population viability analysis seeks to identify those demographic components of a species' life history that most substantially affect long-term persistence. Such analyses generally employ deterministic mathematical models to predict the state of a population at some time in the future, given a set of age- or stage-specific demographic parameters. In general, studies using these methods suggest that even small differences in demographic traits, spatial structure, population size, and levels of dispersal can individually and collectively have a large effect on probabilities of persistence or extinction.

The burrowing owl is widely distributed through arid regions of the western hemisphere, where it usually inhabits burrows initially excavated by fossorial mammals (particularly rodents) or reptiles (Zarn 1974). At one time, the burrowing owl was apparently locally abundant over much of its range, but at least in western North America (and perhaps throughout its geographic distribution), it has substantially declined in numbers since the early 1900s (see Bent 1938, Arbib 1979). In Cali-

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fornia, the burrowing owl was reported to have been common at the turn of the century (Grinnell and Miller 1944). Since then, as its preferred habitat of short grassland has been usurped and fragmented by human development, and as rangeland managers have extensively used rodenticides, burrowing owl numbers have declined, while the distances between populations have increased (unpublished data).

All of these demographic and habitat attributes suggest that the burrowing owl may be particularly sensitive to extinction. Nonetheless, without quantitative information about the demographic traits of burrowing owl populations, it is unclear whether this species will persist locally, and if so, for how long. To begin to answer these questions, I began a demographic, behavioral, and genetic study of a population of burrowing owls in Davis, California, in 1985. Because burrowing owls in my study area had been censused since 1981, I was able to estimate demographic parameters and compare theoretical expectations to the actual trend in population size during a ten-year period.

METHODS

Study Area and Population Size. I studied a population of wild burrowing owls occupying 150 ha of mostly nonnative annual grassland on the campus of the University of California, Davis, California. The owls roosted and nested in burrows excavated by California ground squirrels (*Spermophilus beecheyi*), and they were somewhat habituated to humans, a characteristic that facilitated their study. The grassland tracts were mowed several times during spring and summer for fire control and to improve visibility of the owls with binoculars and spotting scopes.

Changes in the size of this burrowing owl population were measured each year from 1981 through 1991. The total number of territories occupied in each year was determined by spot-mapping (International Bird Census Committee 1970). In 1981–84, T. Schulz of the UC Davis Raptor Center conducted diurnal censuses of adult owls during the breeding season. In 1985–91, I censused adults and juveniles during the reproductive periods and made incidental surveys during some winters.

Burrowing Owl Life History. Like other owls, burrowing owls breed once per year in an extended reproductive period, during which most adults form monogamous pairbonds. However, occasional polygamy and extra-pair fertilizations confound the determination of parentage from field observations (see Johnson 1996b). For estimates of individual reproductive success I therefore incorporated two years of data on genetic parentage, as determined by DNA fingerprinting.

In field studies of burrowing owls during the breeding season, three developmental stages can be identified and monitored: (1) emergent nestlings (up to 3–4 wk old), (2) juveniles, including both fledglings and independent preadults (through age 14–15 wk), and (3) adults. When developing nestlings first emerge from the burrow, they are covered with gray natal down, and they remain near the burrow entrance. A week later, the full-grown nestlings will have molted into a distinctive juvenile plumage in which their heads and backs are solid brown and their breasts and undercoverts are plain beige with no bars. At this time the young owls also begin to fly, becoming competent fliers within 2–3 wk of emergence. Fledgling burrowing owls could be easily identified as such by their plumage until September, by which time they had molted into a cryptic plumage of barred light brown feathers, making them indistinguishable from adults.

Color-Banding and Censusing. I color-banded 112 wild burrowing owls (25 as adults, 87 as juveniles) in 1985–88 during the fledging period (late June through July). Owls were captured with noose carpets and one-way-door traps. Every bird was fitted with a unique combination of 3 colored nylon bands and 1 aluminum U.S. Fish and Wildlife Service band (2 bands per leg). I used a stationary vehicle as a blind and made behavioral observation with binoculars and a spotting scope from distances of between 50–200 m. From direct observations and censuses of all banded and unbanded individuals at least once every two days, I was able to estimate survival rates for juveniles and adults, in addition to individual-specific fecundity for adults of both sexes. Individual reproductive success in 1987–88 was further estimated using DNA fingerprints from 67 of the wild color-banded owls (see Johnson 1996b).

RESULTS

Estimates of Demographic Parameters. I estimated juvenile (s_0) and adult (s) survivorship in three ways, based on data in Table 1, which tracks the survival of unbanded nestlings, juveniles, and adults, in addition to color-banded juveniles and adults, during 1985–89. The survival estimates, denoted "worst case," "intermediate," and "best case," respectively, reflect three increasingly optimistic assumptions: (1) the proportion of the color-banded sample that is known to have survived to the next year accurately represented survival in the population at large, (2) emigration equaled immigration, therefore the number of Davis owls that could have dispersed and survived equaled the number of unbanded adults (putative immigrants) that appeared in the Davis population the next year, or (3) all of the Davis owls that disappeared actually dispersed to survive elsewhere. Estimates based on (1) represent minimum estimates, and they may be the most reliable, especially if the population is closed to emigration and immigration. Estimates that assume (2) are certainly possible, but it is also plausible that unbanded owls were already population members. By this method, population growth was likely overestimated because the survival rate used for each age class assumed

Table 1. Burrowing owl demographic data, 1985–88.

	1985	1986	1987	1988
No. territories	11	12	11	9
No. adults	21[a](7)[b]	23(12)	24(22)	18(16)
Died	0	0	2–5[c](1)	1(1)
Disappeared	18(4)	18(3)	9–12[c](3)	10–12[d](8)
Remain in yr_{t+1}	3(3)	5(5)	10(10)	5–7[d](5–7)[d]
No. emerged nestlings	28(17)	39(21)	24(18)	37(31)
Died (nestlings)	2	2	3	6
Died (juveniles)	2(2)	4(2)	0–3[c](0)	1(1)
Disappeared	20(11)	28(14)	15–18[c](15)	22(22)
Remain in yr_{t+1}	4(4)	5(5)	3(3)	8(8)
No. unbanded adults in $year_{t+1}$	11	2	2	2–4[d]
No. nestlings/adult	1.33	1.70	1.00	2.06
No. successful adults[e]	12	18	15	17
No. nestlings per successful adult	2.33	2.17	1.60	2.06

[a] Includes both color-banded and nonbanded burrowing owls.
[b] Color-banded owls only.
[c] Three unbanded owls that could not be assigned to an age class died in winter 1987. I made one estimate of survivorship as if they had all been adults, and another as if they had all been juveniles.
[d] The discrepancy between the two values is due to two disputable color-band sightings in 1989.
[e] An adult was considered to have successfully reproduced if nestlings emerged from its burrow. Success of 18 owls in 1987–88 was further verified by DNA fingerprinting (see Johnson 1996a).

that all putative immigrants were either juveniles or adults, respectively, in the previous year, rather than a combination of the two. Estimates that assume (3), are extremely optimistic and unlikely; I include them only to define the maximum possible value of reproductive output.

Depending on which assumption they were based, estimates of the probability of juvenile burrowing owl survival, which is equal to the chance of surviving to age at first breeding (1 yr), were 0.23 (worst case), 0.35, or 0.93 (best case). Annual adult survivorship was estimated to be 0.42 (worst), 0.54, or 0.93 (best). I used each set of adult and juvenile survival rates to independently project three different population growth rates, while holding fecundity and age at first reproduction constant.

For the fecundity parameter I estimated the mean *per capita* rate of reproduction, b = 1.49 (±1.251 SD; N = 86), by dividing the number of newly emerged nestlings in 1985–88 by the total number of adults present in those years. I estimated that each pair of owls produced from 0–9 nestlings (0–4.5 offspring per individual). Onset of reproduction in both sexes occurs when owls are one year old and the burrowing owl life cycle is characterized by birth-pulse reproduction (Caughley 1977, Caswell 1989), with an interbirth interval of one year, making it appropriate for modeling in discrete time (Cole 1954).

Projected Population Growth Rate. Using the sets of demographic parameters described above, I determined the theoretical finite rate of growth for the Davis burrowing owl population by solving the Euler-Lotka equation, $1 = \Sigma\ \lambda^{-x} l_x b_x$, for λ. In this equation, l_x is the probability of surviving to age x, and b_x is age-specific fecundity.

Projected population growth rates calculated from the three increasingly optimistic sets of burrowing owl survival rates were 0.8319, 1.0410, and 1.7307. Demonstrable survival rates of banded juveniles and adults produced a value for λ (0.8319) that was much lower than 1.0, indicating a population declining by almost 17% per year. By contrast, the values for λ that were derived from the "intermediate" and "best case" survivorships signify populations increasing by 4% and 73% per year, respectively.

Expected Persistence Time. I calculated the time, in years subsequent to 1981, that the Davis burrowing owl population with an initial size of 44 adults could have been expected to persist if it ex-

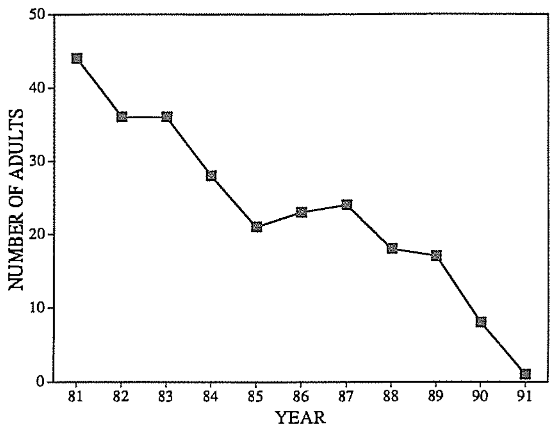

Figure 1. Observed rate of change in numbers of burrowing owls in the Davis population from 1981–91. The number of adults declined from 44 to 1 over the 10-year period.

Table 2. Actual sizes and annual growth rates of the Davis burrowing owl population, 1981–91.

YEAR	NUMBER OF ADULTS	ANNUAL RATE OF GROWTH (λ)
1981	44	—
1982	36	0.8182
1983	36	1.0000
1984	28	0.7778
1985	21	0.7500
1986	23	1.0952
1987	24	1.0435
1988	18	0.7500
1989	17	0.9444
1990	8	0.4706
1991	1	0.1250

perienced a sustained negative rate of change of 0.8319, as analysis with parameters estimated from the sample of color-banded burrowing owls implies it was. Using the formula $T_{extinction} = -\log N/\log \lambda$ (Lande 1985), persistence time for this population was expected to be 20.6 yr.

Observed Population Decline. The actual growth rate for this burrowing owl population was computed directly from the observed population trajectory over the 10-year interval 1981–91. The actual population trend is portrayed graphically in Fig. 1. Total population size (number of adults) in each year and annual growth rates are given in Table 2. I empirically obtained λ, which is equal to the geometric mean of the yearly changes in size, each of which was computed from N_t/N_{t-1}. The actual rate of population change was 0.6849, equivalent to a sustained 31.5% decline since 1981.

DISCUSSION

By using a deterministic approach, I was able to predict the likelihood that the Davis burrowing owl population would become extinct, and over what time scale. The results of this analysis show that the owl population actually declined to extinction in half the time predicted by my most reliable estimates of demographic parameters for owls in 1985–88. However, deterministic analyses assume conditions which are often not upheld by biological populations (i.e., constant vital rates, stable age distribution, closed population). Therefore, some imprecision with this modeling approach is to be expected. In reality, the demographic traits, and consequently the dynamics, of this wild population, and probably most others, can vary in a complex manner.

As shown for the Davis burrowing owls, forces other than systematic ones undoubtedly influenced population dynamics over the 10-year period, to produce a rate of decline 1.88 times that predicted (31.5% compared to 16.8%). Although I used average demographic parameters in my analysis, I observed substantial year-to-year variation in survivorship, with mean annual survival of juveniles varying by 35%, and that of adults by 50%. Similarly, adult fecundity varied among years and between sexes by a factor of two. No conspicuous trends were revealed in either parameter, and the demographic significance to the burrowing owl of such variation in vital rates is not known. However, in keeping with small population theory (Goodman 1987b), if the role of chance demographic events increases with decreasing population size, demographic stochasticity should have been particularly important for an already small population in the last phase of decline.

Other nondeterministic factors could have been important. Two catastrophic climatic events, a drought in 1987–91 and an extended winter freeze in 1990–91, also may have affected vital rates in those years, by causing mass mortality or forcing nomadic dispersal. Drought, in particular, is known to affect the population dynamics of other insectivorous vertebrates (Lack 1968). Due to lack of specific field evidence, however, the importance of these factors to the Davis burrowing owl population remains unclear.

My analysis of burrowing owl population persistence was further limited because it was done out of context of the regional population. Theoretical predictions suggest that larger size should buffer subpopulations against extinction from most stochastic events, whereas regional persistence is enhanced by high numbers of independent subpopulations occupying habitat patches that are separated enough to spread environmental and disease risk, yet close enough to ensure recolonization (Gilpin and Soulé 1986). In any case, dispersal among local populations regulates regional dynamics; unfortunately, it is also one of the most difficult parameters to estimate for wild populations, especially for nocturnal owls.

Little is known about dispersal in the burrowing owl. California populations are primarily resident, with adults and juveniles exhibiting local site fidelity. Root mean square dispersal distances were 0.2 km for adults and 0.5 km for juvenile owls in the Davis population. Based on the sample of color-banded burrowing owls, a very small number of juveniles (2 of 87) dispersed from the study area. However, such movements probably did not result in successful colonization. One juvenile burrowing owl dispersed 1.5 km from its natal burrow to a winter roost under a temporary building at a construction site; it disappeared within 2 wk. The other juvenile dispersed 12 km to landscaped grounds of a residential complex, where it resided in a cement culvert for more than 1 yr, at which time it was still without a mate. Systematic searches of appropriate habitat within 15 km of the Davis population in 1986–89 found none of the color-banded owls that had disappeared from the study area. However, other North American burrowing owl populations are seasonally migratory, with owls flying hundreds of kilometers in winter (Zarn 1974). Some of the Davis burrowing owls may have dispersed long distances, but none of the 80 color-banded owls that disappeared from the Davis population were reported to have been recovered at distant locations.

A further complication in the analysis of population viability is that the dynamics of natural populations are controlled by an interplay between ecological and genetic processes. The methods of viable population analysis used to predict population peristence in this study, and virtually all others, generally do not incorporate the population genetic effects of changing demographies. Importantly, the same ecological processes that directly drive population decline may indirectly exacerbate the likelihood of extinction by inducing changes in the genetic structure of a species. My genetic data suggest that the Davis burrowing owl population is inbred with respect to a hypothetical panmictic population (see Johnson 1996a), but how this might have affected the persistence of my study population, and whether other burrowing owl populations are comparably inbred, remains to be seen. Other studies on spatially-structured populations present equivocal results on the fitness consequences of inbreeding, and as with attempts to assess the effects of genetic variation on fitness, no firm conclusions can be drawn.

As shown by this investigation of burrowing owl dynamics, many processes likely affect population persistence at once. A more comprehensive and robust theory of population dynamics for this species will therefore require a synthesis of the effects of both demographic and genetic processes in a stochastic spatially-structured framework.

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J. Raptor Res. Report 9:34–37

PARAMETERS OF A DECLINING BURROWING OWL POPULATION IN SASKATCHEWAN

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ABSTRACT.—A declining population of banded burrowing owls was studied in Saskatchewan from 1986–92. Annual adult survival increased significantly over the period of study. However, the proportion of pairs that produced young, and the number of chicks produced per nest attempt declined, the former significantly so. In no year was productivity sufficient to offset adult mortality. A simple model predicted the decline of the study population. Despite decreasing over the period of study, the adult mortality rate appeared to be too high, based on body weight and other studies of stable populations. This was exacerbated in some years by poor reproductive success. Juvenile mortality appeared to be normal. The cause of the decline is not known, but excessive predation facilitated by the heavily fragmented habitat is suspected. Other factors may also be operating on the still unknown wintering grounds.

KEY WORDS: *burrowing owl*; Speotyto cunicularia; *status*; *Saskatchewan*; *reproduction*; *mortality*; *Canada*.

Parametros de una poblacion de tecolotito enano en disminucion en Saskatchewan

RESUMEN.—Una poblacion en disminucion de tecolotitos enanos anillados se estudio en Saskatchewan de 1986 a 1992. Sobrevivencia anual de adults aumento significativmente durante el periodo de estudio. Sin embargo la proporcion de parejas que produjeron crias y el numero de pollos producidos por nidada disminuyo, el primero significativamente. En ningun año fue suficiente la productividad para remplazar la mortalidad de adultos. Un modelo sencillo predice la disminucion de la poblacion bajo estudio. A pesar de que la mortalidad de adults disminuyo durante el periodo de estudio, la tasa de mortalidad de adultos parece ser demasiado alta basada en peso y otros estudios de poblaciones estables. Esto se agrava en algunos años de baja reproduccion. La mortalidad de juveniles aparenta ser normal. La causa de la disminucion no se conoce, pero depredacion excesiva facilitada por la gran fragmentacion del habitat se sospecha. Otros factores pueden estar operando en las areas invernantes aun desconocidas.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) is designated as Threatened in Canada by the Committee on the Status of Endangered Wildlife in Canada (Wedgwood 1978, Haug and Didiuk 1991). This means that it is likely to become an endangered species unless the limiting factors operating against it are reversed. Several such factors have been identified (Wedgwood 1978). In 1986, a study was initiated in Saskatchewan to evaluate them in a systematic fashion. To date, studies have been conducted on grasshopper insecticides (James and Fox 1987, Fox et al. 1989, Fox and James 1991), rodenticides (James et al. 1990), and habitat (James et al. 1991, James 1993). We report here on the population dynamics of this study population.

STUDY AREA AND METHODS

The study was conducted on the Regina Plain south of the City of Regina, Saskatchewan (50°27'N, 104°37'W) from 1986–92. The area is mostly devoted to the production of wheat and other crops. The burrowing owls nest on the few remaining highly fragmented and dispersed pastures. Each year, all owl pairs were located, their reproductive success monitored, and as many adults and chicks as possible were captured and banded. Each nesting pair was counted as one nest attempt, and a nest attempt was counted as successful if at least one chick was fledged.

We derived and used the following formula to calculate annual adult survival rates:

$$S_a = [R_t + R_t/C_t(A_t - C_t)]/B_{t-1}$$

where S_a = survival rate of adults, R_t = no. banded adults recaptured in year t, B_{t-1} = no. adults banded in year

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Table 1. Reproductive success of burrowing owls on the Regina Plain, Saskatchewan.

YEAR	NO. NESTS	% SUCCESSFUL[a]	NO. CHICKS/ SUCCESSFUL NEST	NO. CHICKS/ NEST ATTEMPT
1986	99[b]	72	4.3	3.1
1987	221[b]	75	5.3	4.0
1988	55[b]	85	5.3	4.5
1989	54[b]	57	2.9	1.7
1990	39	49	3.4	1.6
1991	37	62	4.8	3.0
1992	29	45	4.0	1.8

[a] Successful = at least one chick fledged.
[b] Includes some nests not in the core study area.

$t-1$, C_t = no. adults captured in year t, and A_t = no. adults available for capture in year t.

The following model was used to predict the size of the population in subsequent years beginning with the 1987 population (Brooks and Temple 1990):

$$N_t = N_{t-1}(S_a) + N_{t-1}(P/2)(S_j)$$

where N_t = size of breeding population in year t, N_{t-1} = size of breeding population in year $t-1$, S_a = survival rate of adults in year $t-1$ (from above), P = number of young fledged per breeding pair in year $t-1$, and S_j = survival rate of juveniles in year $t-1$. Because most surviving young left the study area to breed, it was not possible to estimate S_j in the same way that we could estimate S_a. Two values, 0.20 and 0.30, were therefore used in the modelling. We calculated the lower value from North American general banding returns of burrowing owls (Cave 1968). The higher value was used because this method tends to overestimate mortality (Newton 1979).

RESULTS

Over the seven-year study (Table 1), the proportion of owl pairs that produced at least one chick declined significantly ($r = -0.809$, $P < 0.05$). The number of chicks produced per successful pair, and per nesting attempt also declined, although not significantly ($r = -0.318$ and -0.584, respectively). Annual adult survival ranged between 37% and 51% (Fig. 1), and increased significantly over the period of study ($r = 0.857$, $P < 0.05$).

The population declined steadily from 76 pairs in 1987 to 29 pairs in 1992 (Fig. 2). The rate of decline was highly significant ($r = -0.976$, $P < 0.01$) and fairly constant. The equation of the regression line, $y = 82.8 - 9.5x$, predicts the extinction of the study population in about 1995, assuming that the decline remains linear. The simple population model (Brooks and Temple 1990) pre-

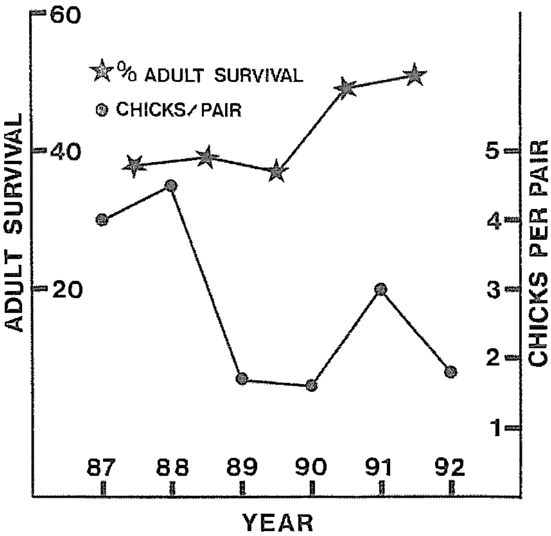

Figure 1. Annual adult survival of burrowing owls and chicks produced per nest attempt on the Regina Plain, Saskatchewan.

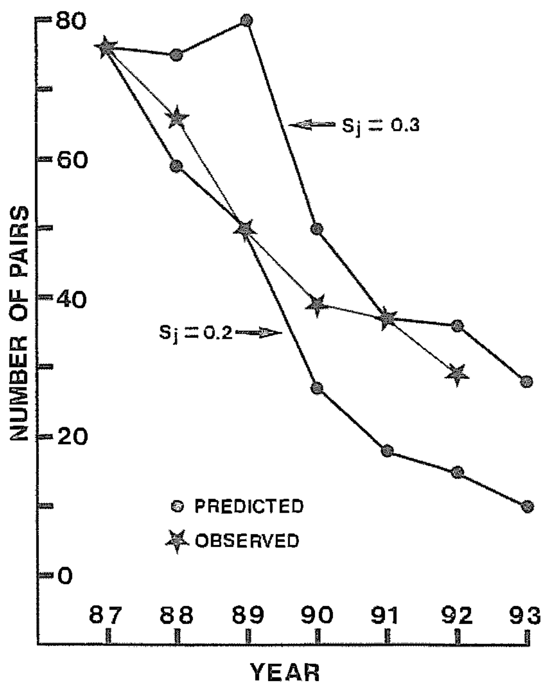

Figure 2. Observed and predicted decline of burrowing owls on the Regina Plain, Saskatchewan. Two predicted declines are shown.

dicted this decline quite well with juvenile survival somewhere between 0.20 and 0.30 (Fig. 2).

DISCUSSION

In no year were enough chicks produced to offset the measured adult mortality; hence, the predicted and observed population decline. Deciding the relative contribution of the three population parameters to this decline is somewhat difficult. Annual adult survival increased over the study period, but was it still too low in the absolute sense? The number of chicks produced per pair declined at the same time, and may have also been too low in an absolute sense. We believe that the adult survival was too low for two reasons. First, on a simple raptor body mass/adult mortality relationship (Newton 1979), our owls appeared to have a mortality rate greater than that expected from body mass alone. Second, our mortality estimates are similar to one calculated for another declining burrowing owl population (Johnson 1995), and much higher than those calculated for more stable populations (Thomsen 1971, Schmutz et al. 1988, Mealey 1997, Millsap and Bear 1995).

We also believe that in some years, the number of chicks produced per nest attempt was too low. Reviews of numerous other breeding productivity studies across North America have shown that the number of chicks produced per nest attempt has fallen below 2.0 only once (Zarn 1974, Haug and Didiuk 1991), yet this has occurred in three of seven years on our study area (Fig. 1).

Evaluating the relative role of juvenile survival is difficult because, unlike adult survival, we could not measure it on the study area owing to natal dispersal being much higher than breeding dispersal. However, if our adult survival and chick production estimates are reasonable, then juvenile survival of our population likely falls between 0.20 and 0.30 (Fig. 2). Based on other studies of more stable populations, this appears to be about right (Thomsen 1971, Millsap and Bear 1995). To investigate this further, we generated theoretical stable population lines by setting $N_t = N_{t-1}$ from the second equation above, and then solved for various values of S_j (Fig. 3). For our population to be stable with the observed adult survival and chick production, S_j would have to fall between 0.3 and 0.4, which is extremely unlikely to occur.

What then, is the cause for our low adult survival and poor chick production in some years? Canadian burrowing owls are migratory, but the location of their wintering grounds is still unknown (James 1992). Because juvenile survival appears normal (Fig. 2, and above discussion), the cause of the reduced adult survival and chick production is probably on the breeding grounds. Although some limiting factors have been evaluated (James 1993, James and Fox 1987, James et al. 1990, James et al. 1991), the role of predation has not. We believe that it could be important for the following reasons: (1) Complete brood failure levels are higher than other studies, and are increasing, while successful pairs have normal production (Table 1) consistent with a pattern produced by predation; (2) The habitat on the Regina Plain is now heavily fragmented, possibly making it easier for predators to find nests; research on nest predation has shown that it increases with increasing habitat fragmentation (Wilcove 1985, Terborgh 1989, Johnson and Temple 1990, Burger et al. 1994); (3) Several mammals that depredate nests of prairie birds, including burrowing owls, are very common in and around the study area (Sargeant et al. 1993).

We therefore hope, in the near future, to evaluate the role that predators may be playing in the decline of the burrowing owl in Saskatchewan.

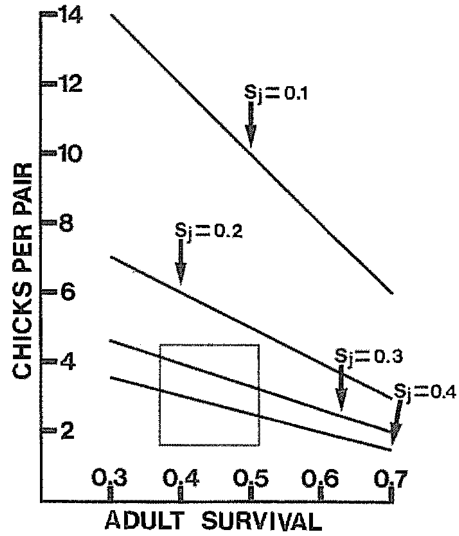

Figure 3. Theoretical stable population lines ($N_t = N_{t-1}$) for various values of S_j (juvenile survival). The window shows the observed values of adult survival and chicks produced per nest attempt on the Regina Plain, Saskatchewan.

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NOTE ADDED IN PROOF

The population continued its decline in 1993 as predicted in Fig. 2. In 1994, the Wildlife Branch of Saskatchewan Enviroment and Resource Management began a supplementary feeding program to boost the number of chicks produced. While still preliminary, the results indicate that the population has stabilized in 1995 and 1996.

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J. Raptor Res. Report 9:38–48

A CENSUS OF BURROWING OWLS IN CENTRAL CALIFORNIA IN 1991

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Abstract.—The Institute for Bird Populations, with the help of 13 local Audubon Society chapters and ornithological organizations, conducted a census of burrowing owls (*Speotyto cunicularia*) in central California between 15 May and 15 July 1991. This 43 425-km^2 census area was divided into 1792 5-km by 5-km blocks oriented to the Universal Transverse Mercator system. Censuses were completed on a random stratified sample of 197 of these blocks and on 82 additional blocks that were not randomly chosen but were known to contain presumed breeding owls during the preceding decade. An analysis of these data suggests that: (1) the total breeding population of burrowing owls in the central California census area in 1991 may be estimated at about 873 pairs; (2) decreases of at least 23% of the breeding groups and 12% of the breeding pairs occurred during the five years 1986–91; (3) the rate of decline of breeding burrowing owls appeared to be greatest in the Outer Coast region, less in the Bay Area region, and least in the Central Valley region; (4) the number of pairs per breeding group also appeared to decrease, especially in the Bay Area region; and (5) the species was extirpated as a breeding bird from Sonoma, Marin, Napa, and Santa Cruz Counties during the decade 1981–91. We suggest that loss of breeding habitat may be a major cause for this population decline, but other factors may also have contributed to it. If the population trends indicated for the late 1980s continue, concerted efforts to reverse these trends will be necessary to prevent the species from becoming extirpated in central California.

Key Words: *burrowing owl;* Speotyto cunicularia; *random stratified census; population estimate; population trends; California.*

Un censo del tecolotito enano en el centro de California en 1991

Resumen.—El Instituto de Poblaciones de Aves con la ayuda de 13 sociedades locales de Audubon y organizaciones ornitologicas condujo un censo del tecolotito enano, *Speotyto cunicularia* en el centro de California durante Mayo 15 a Julio 15 de 1991. El area censada que comprendia 43,425 km^2 se dividio en 1,792 cuadros de 5 km × 5 km orientados al sustema UTMS. Censos se completaron de manera estratificados al azar en 197 de los cuadros y 82 cuadros adicionales no seleccionados al azar sino en base al conocimiento de que estos contenian poblaciones reproductivas durante la decada anterior. El analisis de estos datos sugiere que: 1) La poblacion reproductiva total del tecolotito enano en el area censada en 1991 se estimo en aproximadamente 807 parejas; 2) Disminucion de cuando menos 23% de grupos reproductivos y 12% de parejas reproductivas occurio en los 5 años de 1986–1991; 3) La tasa de disminucion de tecolotes reproductores parece ser mayor en el area costera, menos en la region de la Bahia y menor en el area del Valle Central; 4) El numero de parejas reproductoras parece especialmente en el area de la Bahia; 5) La especie se ha extirpado como ave reproductora de los condados de Sonoma, Morin, Napa y Santa Cruz durante la decada de 1981–1991. Sugerimos que la principal causa de la disminucion de esta poblacion es la perdida de habitat reproductivo, pero otros factores pudieron haber contribuido. Si continua la tendencia indicada en los ultimos años de los 1980's esfuerzos concertados seran necesarios para prevenir que la especie sea extirpada del centro de California.
[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) is a characteristic species of flat, open grasslands at lower elevations nearly throughout California. The species has been undergoing a general population decline in California (and elsewhere in its range) for at least the past 60 years, generally as a result of "roadside shooting, anti-"vermin" campaigns, [and the] elimination of ground squirrels—hence of nesting places for these owls" (Grinnell and Miller 1944).

Within the past 20 years, however, the decline of burrowing owls in California appears to have accelerated, apparently as a result of habitat loss caused by the increased residential and commercial development of land that has paralleled the phenomenal growth of California's human population (McCaskie et al. 1979, Garrett and Dunn 1981). Indeed, it appears that certain characteristics of suitable burrowing owl nesting habitat (open, flat grassland at lower elevations) are very similar to the characteristics of land preferred for residential and commercial development. Because current indicators predict that California's extraordinary human population growth will continue during the 1990s and into the next century, the amount of burrowing owl habitat available and, thus, the size of burrowing owl populations in California can be expected to decline further.

The burrowing owl is currently classified by the California Department of Fish and Game as a "species of special concern," a classification that provides a stimulus for further study and a basis for limited habitat protection of the species. Although various individuals and organizations have suggested informally that a classification of "threatened" may be warranted, adequate data on which to base estimates of local, regional, and total population sizes as well as estimates of population trends are not available for burrowing owls in California. It is evident, therefore, that a census of California's burrowing owl populations, along with a follow-up program to monitor these populations, is justified.

A program of censusing and monitoring California's burrowing owls has a number of attractive components. Because burrowing owls are easily identified, relatively easily counted, and are favorite birds for many bird watchers, large locally-based volunteer efforts can provide accurate counts and exact locations for a substantial proportion of the local breeding populations, critical information on population changes, and useful data on habitat utilization for the species. Information on local and regional distributions and population changes of burrowing owls can be used to inspire local and regional planning processes that are crucial to the development of a sound conservation program for the species.

Detailed information on the exact numbers and locations of breeding burrowing owls over a substantial portion of their California breeding range during three consecutive years can be combined with detailed land-use information available from the California Department of Water Resources by means of Geographic Information Systems (GIS). These combined data can be used to define and evaluate the critical habitat requirements of the species, to estimate the total amount and distribution of potentially suitable habitat, and to estimate the total population size of the species. Such a technique has recently been used to estimate the total population size of the California gnatcatcher (*Polioptila californica*) (Atwood 1992).

In light of these considerations, we designed a three-year (1991–93) census and a follow-up, long-term monitoring program to determine population estimates and trends, to locate critical breeding areas, and to determine general habitat requirements for the burrowing owl in California. For practical and logistical considerations and in order to test the methods and refine the techniques, the first year of the census was limited to central California. The census was expanded in the second and third years to include all of the breeding range of the burrowing owl in California exclusive of the Great Basin and desert areas.

Here we report on the first year of the census, provide an estimate of the size of the 1991 breeding population in central California, and, based on previous anecdotal data on the numbers and locations of presumed breeding pairs, provide estimates of population trends for the species over the past half-decade (1986–91).

METHODS

Census Design and Sampling Considerations. The Institute for Bird Populations, in association with 13 local Audubon Society chapters and ornithological organizations in the San Francisco Bay area and the central part of the Central Valley of California, coordinated the establishment of a census of burrowing owls in central California. The focus of the 1991 census was an area of about 43 425 km^2 bounded by Sonoma, Napa, Yolo, Sacramento, and El Dorado Counties inclusive on the north; by Santa Cruz, Santa Clara, Merced, and Mariposa Counties inclusive on the south; by the 610-m contour line in the Sierra Nevada Mountains on the east; and by the Pacific Ocean on the west (Fig. 1). This area was apportioned among the 13 cooperating organizations according to their geographical areas of interest, which often were defined by county boundaries.

A local area coordinator was appointed by each cooperating organization. These area coordinators provided prior anecdotal information on breeding burrowing owls by plotting the exact locations and approximate numbers of all burrowing owls known or assumed to have bred in the area during the past five years (1986–90) on county

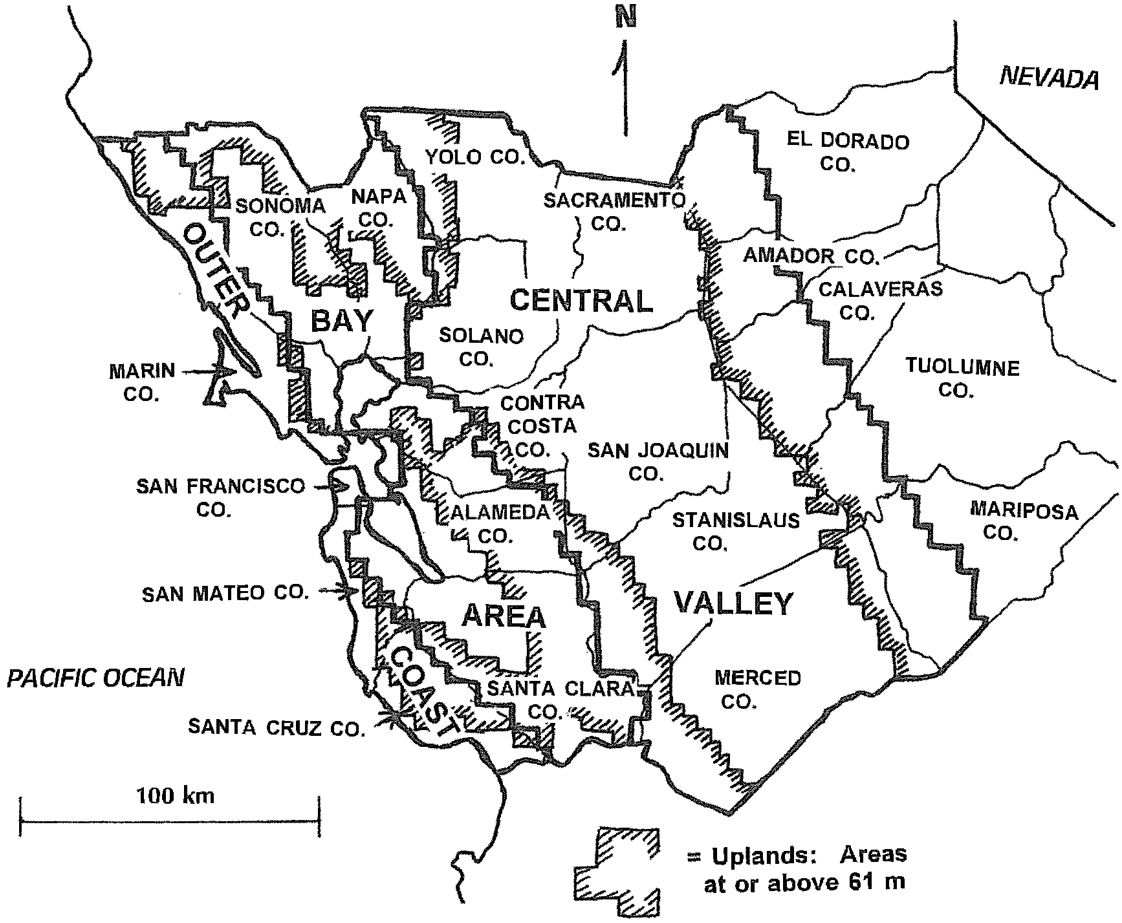

Figure 1. Map of the 1991 burrowing owl census area in central California showing the three geographic regions into which the census area was divided (Outer Coast, Bay Area, Central Valley) and the two elevation subregions into which each region was divided (lowland–below 61 m, upland–61 m and above).

(or other) maps. Locations of owls known or assumed to have bred in the area during the prior five years (1981–85), but that had disappeared by 1986, were also marked on the maps and indicated as such. Breeding at a given location was assumed if: (1) one or more adult owls were found during the breeding season (March–August); or (2) one or more owls were found during the non-breeding season (September–February), the nonbreeding-season location contained suitable breeding habitat, and historical information indicated that burrowing owls regularly bred in such habitats and at such locations in that general area of the county. Although the area coordinators used all available information to identify locations of presumed breeding (e.g., Suddjian and Rigney 1988), the compilations they supplied were understandably incomplete.

We divided the entire census area into three geographic regions (Fig. 1). The Outer Coast region extended west from the crest of the outermost coast range to the Pacific Ocean and also included most of Berkeley and northern Oakland. It thus coincided with those areas most heavily affected by extensive summer fogs. The Bay Area region extended east from the eastern edge of the Outer Coast region to the crest of the innermost coast range. This area encompassed most of the greater San Francisco Bay area and associated interior valleys, including the Petaluma, Sonoma, Napa, Walnut Creek, Livermore, and Santa Clara valleys. The Central Valley region extended east from the eastern edge of the Bay Area region to the 610-m contour line in the Sierra Nevada Mountains.

We divided each of these three geographic regions into two elevational sub-regions: that portion below 61 m and that portion 61 m and above (Fig. 1). In the central California census area under consideration, the 61-m elevation contour generally accurately discriminates between the relatively wide, flat lowlands and valley bottoms (where the vast majority of the agricultural and industrial

Table 1. Number of 5-km by 5-km census blocks (and % adequately completed) by geographic-elevation region and type for the 1991 census of burrowing owls in central California.

	RANDOM[a]			OWL[b]			TOTAL[c]		
	LOWLAND[d]	UPLAND[e]	TOTAL	LOWLAND	UPLAND	TOTAL	LOWLAND	UPLAND	TOTAL
Outer Coast	30 (86.7)	8 (87.5)	38 (86.8)	4 (75.0)	0 (—)	4 (75.0)	34 (85.3)	8 (87.5)	42 (85.7)
Bay Area	36 (80.6)	29 (62.1)	65 (72.3)	50 (72.0)	2 (50.0)	52 (71.2)	77 (74.0)	30 (63.3)	107 (71.0)
Central Valley	137 (65.7)	44 (61.4)	181 (64.6)	89 (79.8)	5 (80.0)	94 (80.0)	203 (69.0)	45 (60.0)	248 (67.3)
Total	203 (71.4)	81 (64.2)	284 (69.4)	143 (76.9)	7 (71.4)	150 (76.7)	314 (72.0)	83 (63.9)	397 (70.3)

[a] Blocks randomly selected (about 20% of lowland and 10% of upland blocks).
[b] Blocks that contained presumed breeding owls sometime during 1981–90.
[c] Because some random blocks previously contained breeding owls, the number of random blocks plus the number of owl blocks may be greater than the total number of blocks.
[d] Lowland blocks in which at least 5% of the area lay below 61 m elevation.
[e] Upland blocks lying above 61 m elevation.

development and a major portion of the residential development occurs) and the upland hills and mountains. The distribution of presumed breeding locations supplied by the area coordinators suggested that burrowing owl breeding habitat in central California may be essentially limited to the flat lowlands and valley bottoms of the area. The 61-m elevational division allowed us to test this hypothesis.

For sampling purposes, we divided the entire 43 425-km^2 census area into 1792 5-km by 5-km blocks oriented and referenced according to the Universal Transverse Mercator (UTM) system. We used a random number generator to chose 20% of the blocks in each geographic region (Outer Coast, Bay Area, Central Valley) that contained at least 125 ha (5% of its area) under 61 m elevation. A total of 203 of these "lowland blocks" was randomly chosen out of the 1012 total lowland blocks in the census area. We then randomly chose 10% of the blocks in each region that did not contain at least 125 ha under 61 m elevation, with the additional requirements that the chosen block contain at least 25 ha of open, nonscrub, nonforested area and that the block be accessible by automobile. A total of 81 of these "upland blocks" was randomly chosen out of the 780 total upland blocks in the census area. This gave us a total random stratified sample of 284 blocks termed "random blocks" (Table 1).

Next we plotted the locations where burrowing owls were presumed to have bred during the past ten years on five 1:250 000 scale U.S.G.S. maps that covered the census area and on which we had drawn the 1792 5-km by 5-km UTM blocks. These locations were found to occur in a total of 150 blocks which were termed "owl blocks" (Table 1). Thirty-seven of the 150 owl blocks (24.7%) had already been chosen as part of the sample of 284 random blocks; these were termed "random owl blocks." The remaining 113 owl blocks that were not chosen as part of the random sample, termed "non-random owl blocks," were then added to the random sample of 284 blocks and produced a total sample of 397 census blocks. The remaining 247 random blocks in which owls were not presumed to have bred during the past ten years were termed "random non-owl blocks."

We marked and physically cut the 397 5-km by 5-km UTM census blocks out of 1:24 000 scale U.S.G.S. topographic maps (7.5-min series). These cut-out census blocks were each placed in packets that also included a "locator map" (a portion of a 1:250 000 scale U.S.G.S. map), a specially-prepared 12-page instruction and information booklet on censusing burrowing owls, and appropriate data sheets. We apportioned the 397 census blocks among the 13 cooperating organizations and distributed the completed packets to the area coordinators who, in turn, distributed them to volunteer censusers that they recruited. To provide in-the-field instruction and training for both the area coordinators and the volunteer censusers, four half-day training sessions were held prior to the census in late April.

Field Work. The volunteer censusers were asked to cover all of the area in their blocks at least once during early-morning (dawn to 1000 H) or late-afternoon (1600 H to dusk) hours during the 2-mo period between 15 May and 15 July, when breeding burrowing owls were likely to be feeding nestlings or recently-fledged young. During these times, one or both parents are usually readily observable at or near the mouth of the nest burrow. Censusers were asked to search their blocks as thoroughly as possible for burrowing owls, and to operate under the assumption that burrowing owls are, or should be, present, and that the censuser's job is to find them or to prove that they are not there.

Censusers were asked to classify the various areas contained in their block into one of three categories depending on the extent of their coverage of them: inadequate, adequate, or thorough. Areas were considered adequately covered if a reasonable effort was made to search all locations where burrowing owls were likely to be breeding. Areas were considered thoroughly covered if the censuser felt confident that her/his estimate of the number of breeding pairs of owls was correct and that all breeding owls were located. Censusers were also asked to provide a narrative and standardized information on the amount and timing of effort they expended on their block.

Censusers were asked to provide: (1) a count of all owls seen in their block, identified, if possible, to age and sex; (2) an estimate of the number of nesting pairs; (3) the exact locations of all owls seen plotted directly on the U.S.G.S. topographic map of their block; and (4) standardized habitat information at all locations where they found owls.

Data Analysis. We transcribed the exact locations of all burrowing owls presumed to have bred in the census area during the previous ten years (1981–90) directly onto the completed U.S.G.S. 7.5-min topographic maps of each of the owl blocks. Because we wanted to obtain an unbiased population estimate from the random sample of blocks and did not want to bias the coverage of owl blocks, particularly the coverage of random owl blocks, we did not transcribe prior owl locations onto maps before sending them out for censusing.

We used data from the 1991 census to obtain estimates for the total number of breeding pairs of burrowing owls in 1991 in each geographic-elevation region and then summed these estimates to obtain an estimate for 1991 for the entire census area. We used two methods to obtain these regional estimates. In the first method, we used data from all random blocks but did not use data from nonrandom owl blocks. We estimated $N1_i$, the total number of pairs of owls in the ith (geographic-elevation) region from Method I as $N1_i = nr_i * (1/pr_i)$ where nr_i is the total number of pairs counted in 1991 in all of the random blocks that were adequately or thoroughly censused in the ith region and pr_i is the proportion of the total area of the ith region that was contained within all of the random blocks in the ith region and that was adequately or thoroughly censused.

In the second method, we used data from only the random non-owl blocks (rather than from all the random blocks) and then added data from the owl blocks. In this case we estimated $N2_i$, the total number of pairs of owls in the ith region from Method II as $N2_i = N2n_i + N2o_i$ where $N2n_i$, the total number of pairs in all the non-owl blocks in the region, is calculated as $N2n_i = nrn_i * (1/prn_i)$ where nrn_i is the total number of pairs counted in 1991 in all of the random non-owl blocks that were adequately or thoroughly censused in the ith region and prn_i is the proportion of the total area of all the non-owl blocks in the ith region that was adequately or thoroughly censused, and where $N2o_i$, the total number of pairs in all owl blocks in the region, is calculated as $N2o_i = no_i * (1/po_i)$ where no_i is the total number of pairs counted in 1991 in all of the owl blocks that were adequately or thoroughly censused in the ith region and po_i is the proportion of the total area of all the owl blocks in the ith region that was adequately or thoroughly censused. Those portions of the blocks that fell in the Pacific Ocean or San Francisco Bay were not included in calculating any of the areas used in these estimations.

Estimates of the total number of breeding pairs of owls obtained from these two methods in any region will differ somewhat depending on the distribution of owls in the region and the proportion of owls whose locations were actually known prior to the 1991 census. If owls tended to be underdispersed (clumped) in any region and the locations of a large proportion of the owls in the region were known prior to the 1991 census, estimates from Method II will generally be larger and probably more accurate. This was likely the situation in the Bay Area and Outer Coast regions. In contrast, in areas where the owls tended to be overdispersed (more uniformly distributed) and a relatively small proportion were known prior to 1991 (as was probably the case in the Central Valley region), Method I will generally produce larger and probably more accurate estimates. We estimated the total population size of breeding owls in the entire census area by summing the larger of the two estimates for each region over all six geographic-elevation regions.

Finally, we used data provided by the area coordinators on the presumed breeding locations of burrowing owls in the census area in the 5-yr period 1986–90, coupled with the results of the 1991 census, to estimate changes in the numbers of breeding pairs of owls between these two time periods in each of the three geographic regions and for the census area as a whole. Because burrowing owls appear to move their breeding sites over short (2–3 km) distances from year to year as conditions change, but do not appear to move over larger distances (A. Huffman and D. DeSante unpubl. data), we apportioned all of the known and presumed breeding locations of burrowing owls into "breeding groups." Any location found within 3.0 km of any other location in continuous breeding habitat, or within 2.0 km of any other location from which it was separated by non-breeding habitat, was considered to be part of the same breeding group. This procedure effectively apportioned breeding locations into breeding groups; in fact, most owl locations were found to lie either well within 2 km or well over 3 km of each other.

We then used these breeding groups as the appropriate units to determine population changes from the 1986–90 period to 1991. We calculated the number and proportion of groups that disappeared by 1991, that remained in 1991, and that were newly found in 1991. Then, for each region and for the entire census area, we calculated changes in the numbers of groups and in the numbers of pairs in each of these groups. Because the data for the 1986–90 period were not derived from a systematic census but rather from anecdotal information, many of the new groups and pairs within those new groups that were found in 1991 were likely present during 1986–90 but were unknown at that time. Thus, we calculated changes between 1986–90 and 1991 in the numbers of groups and pairs by two methods: (1) including and (2) excluding data from newly-found groups.

RESULTS

Effort Expended. A total of 279 blocks (70.3% of the 397 blocks sent out) was adequately or thoroughly censused during the summer of 1991 (Table 1). In addition, 9 blocks (2.3%) were censused and returned but the effort over the entire block was considered inadequate. An additional 85 blocks (21.4%) were returned but not censused, and 24 blocks (6.0%) were never returned. It is likely that most of these 24 outstanding blocks were not censused. A total of 2111 person-hours was spent surveying the 279 adequately-censused blocks for an average effort of 7.57 hr per block. In all, a total area of 6195 km^2 was adequately

Table 2. Estimates of the numbers of breeding pairs of burrowing owls in the central California census area in 1991.

	OUTER COAST		BAY AREA		CENTRAL VALLEY		
	LOWLAND[a]	UPLAND[b]	LOWLAND	UPLAND	LOWLAND	UPLAND	TOTAL
I. Method I (using all random blocks)							
nr (pairs in random blocks)	0	0	9	0	86	1	96
pr (proportion of area censused)	0.170	0.080	0.143	0.062	0.123	0.052	
N1 (estimate of total population)	0.0	0.0	62.8	0.0	698.0	19.1	
II. Method II (using random non-owl blocks and all owl blocks)							
A. Estimate in non-owl blocks							
nrn (pairs in random non-owl blocks)	0	0	0	0	27	1	28
prn (proportion of area censused)	0.185	0.080	0.131	0.062	0.109	0.047	
N2n (estimate in non-owl blocks)	0.0	0.0	0.0	0.0	247.9	21.5	
B. Estimate in owl blocks							
no (pairs in all owl blocks)	0	0	98	5	205	0	308
po (proportion of area censused)	0.817	—	0.687	0.500	0.753	0.520	
N2o (estimate in owl blocks)	0.0	0.0	142.7	10.0	272.3	0.0	
C. Estimate in total census area (A + B)							
N2 (estimate of total population)	0.0	0.0	142.7	10.0	520.2	21.5	
III. Final estimate (using larger estimate for each region)							
N (estimate of total population)	0.0	0.0	142.7	10.0	632.2	21.5	806.4
n (total pairs found in 1991)	0	0	98	5	232	1	336
% pairs known in 1991	—	—	68.7	50.0	36.7	4.7	41.7

[a] Lowland blocks in which at least 5% of the area lay below 61 m elevation.
[b] Upland blocks lying above 61 m elevation.

searched for burrowing owls during the 1991 census. Table 1 shows that overall the Outer Coast received somewhat better coverage (85.7% of blocks adequately censused) than the Bay Area (71.0%) and Central Valley (67.3%), lowland blocks received slightly better coverage (72.0%) than upland blocks (63.9%), and owl blocks received slightly better coverage (76.7%) than random blocks (69.4%).

Number of Owls Found and an Estimate of the Total Breeding Population. No breeding burrowing owls were found in 1991 in the Outer Coast region, 103 pairs were found in the Bay Area region, and 233 pairs were found in the Central Valley region, resulting in a total of 336 pairs in the total census area (Table 2). Fully 330 of these 336 pairs were found in lowland blocks.

Estimates derived from two methods (see Methods section) for the number of breeding pairs of burrowing owls in 1991 in each of the six geographic-elevation regions and in the total central California census area are presented in Table 2. As perhaps expected, Method II (using random non-owl blocks and owl blocks separately) gave higher estimates for all regions except the Central Valley lowlands where many owls still exist but relatively few of them were previously known. Indeed, Method I actually underestimated the known numbers in regions where most of the owls were already known, as was the case in both Bay Area subregions.

Using the larger of the estimates from the two methods for each region, Table 2 estimates that, as of 1991, no breeding pairs of burrowing owls existed in the Outer Coast region, only about 153 breeding pairs existed in the Bay Area region, and only about 720 breeding pairs existed in the Central Valley region, resulting in a total of only about 873 breeding pairs in the entire central California census area. Moreover, as of 1991, the locations of 67.5% of the pairs estimated to be present in the Bay Area region, 32.4% of those estimated to be present in the Central Valley region, and 38.5% of those estimated to be present in the entire census area were known.

Apparent Population Decline of Breeding Burrowing Owls in the Census Area. The 1991 census failed to find burrowing owls in 59 (51.3%) of the 115 owl blocks that were adequately censused and returned, suggesting that, in the 10 years 1981–90, the proportion of the census area occupied by breeding burrowing owls decreased by about 50%. Indeed, our data indicate that, as of 1991, burrowing owls had been extirpated as breeding birds from Sonoma, Marin, Napa, and Santa Cruz Counties.

These results, however, do not necessarily imply that a 50% decline has occurred in the total population of breeding burrowing owls in central California. Rather, it is possible that owls are now occupying blocks in which they were formerly absent and that the 50% decline in occupied owl blocks represents a shifting of the population rather than a population decline. Such a scenario, however, seems unlikely to account for the number of blocks from which owls disappeared, because previously unknown owls were found in 1991 in only 15 (9.1%) of the 164 random non-owl blocks adequately censused. Moreover, all 15 of these "new owl blocks" were located in the Central Valley region where the distribution of owls was relatively poorly known prior to the 1991 census. In contrast, three of the 59 blocks from which all owls disappeared were located in the Outer Coast region and 21 were located in the Bay Area region. Furthermore, owls were not found in 1991 in any of the 33 random non-owl blocks adequately censused in the Outer Coast region nor in any of 39 similar blocks in the Bay Area region.

It is also possible that the blocks from which burrowing owls disappeared were areas of somewhat marginal habitat that previously supported only a few breeding pairs and that the total number of breeding pairs in central California has not declined precipitously. We can test this hypothesis by analyzing changes between the 1986–90 period and 1991 in the actual numbers of breeding groups (as defined in the Methods section) and pairs of owls. As discussed in the Methods section, this analysis was accomplished in two ways, first by excluding and then by including blocks in which owls were not known prior to 1991 but were found in 1991.

The results of these analyses indicate that, when

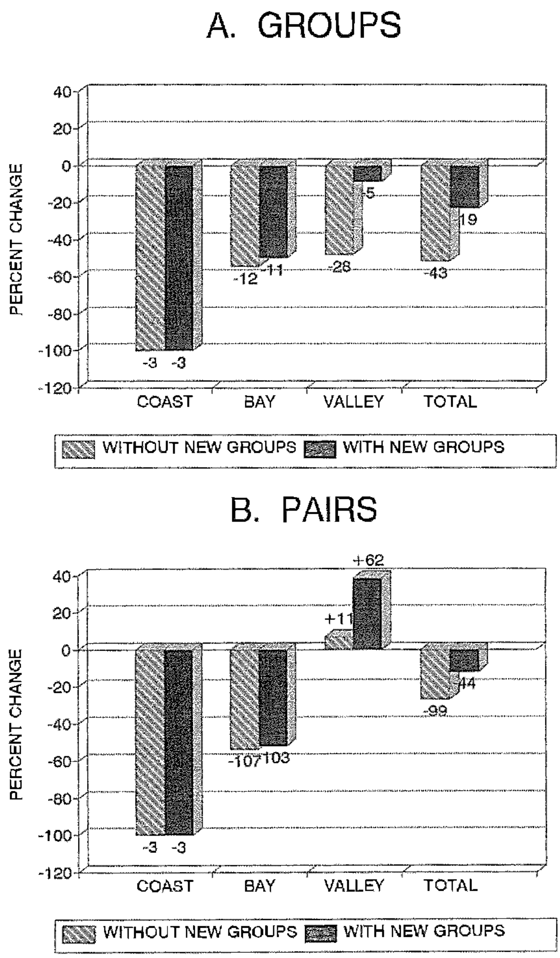

Figure 2. Percent changes in the numbers of (A) groups and (B) pairs of burrowing owls from the 1986–90 time period to 1991 for each geographic region (Outer Coast, Bay Area, Central Valley) and for the entire central California census area (Total). Changes were calculated by two methods: excluding and including newly-found groups of owls (see text). Numbers below (or above) each bar are the actual changes in numbers of groups or pairs.

new owl blocks were excluded, the changes in the number of breeding groups of owls (Fig. 2A) were −100.0% for the Outer Coast region, −54.5% for the Bay Area region, −48.3% for the Central Valley region, and −51.8% for the entire census area. When new owl blocks were included in the analysis, the changes in the number of breeding groups of owls were −100.0% for the Outer Coast region, −50.0% for the Bay Area region, −8.6% for the

Table 3. Estimates of the number of pairs of burrowing owls per breeding group obtained from the 1991 census and anecdotal information during the prior five years (1986–90).

	OUTER COAST		BAY AREA		CENTRAL VALLEY		TOTAL	
	1986–90	1991	1986–90	1991	1986–90	1991	1986–90	1991
For groups that disappeared	1.00	—	2.67	—	1.36[a]	—	1.70[b]	—
For groups that remained	—	—	16.60	9.10	4.10[a]	5.73	7.22[b]	6.58
For newly-found groups	—	—	—	4.00	—	2.22	—	2.39
For all groups combined	1.00	—	9.00	8.64	2.78[a]	4.21	4.36[b]	4.97

[a] Probably biased low because of very incomplete information on the numbers of pairs breeding previously.
[b] Probably biased low because of low-biased estimates from the Central Valley region.

Central Valley region, and −22.9% for the entire census area. The smaller decreases found when new owl blocks were included, especially in the Central Valley region, reflects the fact that not all breeding groups of owls were known prior to the 1991 census. The actual rates of change probably lie somewhere between the extremes produced by the two methods. Anecdotal information supplied by area coordinators further describes the disappearance of 14 presumed breeding owl groups in the Bay Area region and 11 in the Central Valley region between the 1981–85 and 1986–90 time periods. This indicates that the apparent decline of owls was already underway during the first half of the past decade.

Changes in the number of breeding pairs of owls (Fig. 2B), when new owl blocks were excluded, were −100.0% for the Outer Coast region, −54.0% for the Bay Area region, +6.8% for the Central Valley region, and −27.3% for the entire census area. When new owl blocks were included in the analysis, the changes in the number of breeding pairs of owls were −100.0% for the Outer Coast region, −52.0% for the Bay Area region, +38.5% for the Central Valley region, and −12.2% for the entire census area. Again, the smaller decreases (or larger increases in the Central Valley region) found when new owl blocks were included reflects the fact that the actual numbers of breeding pairs of owls were very poorly known prior to the 1991 census, especially in the Central Valley region. The actual rates of change again probably lie somewhere between the extremes produced by the two methods. And again, anecdotal information supplied by area coordinators describes the disappearance of 22 presumed breeding pairs of owls in the Bay Area region and 11 in the Central Valley region between 1981–85 and 1986–90.

Estimates of the number of pairs of burrowing owls per breeding group (group size) were obtained from the 1991 census and from anecdotal information during the prior five years, 1986–90 (Table 3). In each geographic region, group size was smallest for groups that disappeared, intermediate for newly-discovered groups, and largest for groups that remained. This suggests that groups that disappeared were smaller than average, probably were previously reduced in size, and possibly tended to be located in marginal habitats or near the edges of the species range in central California. Group size for groups that remained decreased markedly between 1986–90 and 1991 in the Bay Area region and over the entire census area but appeared to increase in the Central Valley region. This latter apparent increase was probably caused by the fact that group size was very poorly known in the Central Valley prior to the 1991 census and likely was seriously underestimated. For example, in the Central Valley, the number of pairs at many of the presumed breeding locations that were mapped by the area coordinators were not known; in these cases, we assumed that only one pair of owls was present at a breeding location. The overall reduction in group size between 1986–90 and 1991 for groups that remained suggests that population decreases also occurred in optimal habitats and in the heart of the species' range in central California as well as in marginal habitats and on the periphery of the range.

DISCUSSION

Estimate of the Total Breeding Population. Results of the 1991 census indicate that the total 1991 population size of burrowing owls in the central California census area was small, perhaps only about 873 pairs, and that the locations of a substantial proportion of these (a total of 336 pairs, 38.5%) were known in 1991. Information on these known pairs will be very important in efforts to protect the owls, and every effort should be expended to locate as many as possible of the remaining pairs of owls in central California.

In addition, only three groups comprising six total pairs of owls were found in only two blocks that lay entirely above 61 m in elevation; two of these groups and five of these pairs were located in a single block in the Livermore area. This block was, in fact, the only block in the entire Bay Area region where breeding owls were found substantially removed from the immediate vicinity of San Francisco Bay. These results confirm that very few burrowing owls breed in central California at elevations above 61 m, and that the species seems to be virtually confined to the flat, lowland portion of the Bay Area and Central Valley regions. Such areas, moreover, are the areas that are being increasingly used for new residential and commercial development.

It is also of considerable interest that burrowing owls were apparently extirpated as breeding birds during the past decade from Sonoma, Marin, Santa Cruz, and Napa Counties, and only one breeding pair apparently still existed in San Mateo County in 1991. The population around the north end of San Francisco, San Pablo, and Suisun Bays was also reduced to a very small remnant, if indeed it still existed at all. It appears, therefore, that breeding burrowing owls in central California have been, or very soon will be, reduced to only three isolated populations: a moderate but declining population of about 720 pairs in the Central Valley, a small and rapidly declining population of about 143 pairs in the lowlands around the southern arm of San Francisco Bay between Alameda and Redwood City, and a very small, isolated population of about 10 pairs in the Livermore area. Such population fragmentation will very likely further increase the species' risk of extirpation.

Estimates of Recent Population Change. The results of the 1991 census, coupled with anecdotal information from 1986–90, suggest that the net population change between these two time periods was a decrease of about 23–52% in the number of breeding groups and about 12–27% in the number of breeding pairs of owls. A more exact estimate of population change cannot be obtained because of the incomplete and anecdotal nature of the information on breeding burrowing owls prior to the 1991 census. The overall decreases of both breeding groups and breeding pairs, however, appeared to be greatest in the Outer Coast region (100% for both groups and pairs), less in the Bay Area region (about 53% for both groups and pairs), and least in the Central Valley region (perhaps about 28% for groups and an increase of about 23% for pairs). It seems likely that the loss of most of these breeding groups and many of these breeding pairs was caused primarily by the loss of breeding habitat.

Data from the 1991 census and prior anecdotal information during the period 1986–90 suggest that the number of pairs per breeding group (group size) also decreased in at least the Bay Area region (and probably also in the Central Valley region). This suggests that some other factors in addition to habitat loss may be contributing to the decrease in burrowing owls in central California. Although we have no direct data to support the hypothesis, we suspect that various agricultural practices, including removal of ground squirrels, use of chemical herbicides on levees along irrigation canals, and the more general use of chemical insecticides and rodenticides may also be contributing to the observed declines of burrowing owls in central California.

Such agricultural practices could adversely affect the productivity and survivorship of burrowing owls. In this regard, it may be worth noting that the number of young fledged from burrowing owl nests in central California in recent years seemed to vary between three and six, with most nests fledging only four or five young (pers. obs.). Anecdotal accounts of nesting burrowing owls in California during the first half of this century suggest that six to eight young were usually fledged (Dawson 1923). Indeed, other avian predators in central California, including loggerhead shrike (*Lanius ludovicianus*), American kestrel (*Falco sparverius*), and Swainson's hawk (*Buteo swainsoni*), also appear to be declining as breeding birds in recent years in central California (R. Stallcup pers. comm.). The first two species, like burrowing owls, rely heavily on large insects in their diet during the breeding season and forage in similar grassland habitats.

Sources of Error in Estimates of Population Size and Change. A number of factors could have contributed to errors in this census: (1) limitations of the pre-1991 data that were supplied to us by the area coordinators; (2) inaccuracies in the 1991 census itself; and (3) misinterpretation of the data from the 1991 census. It must be stressed that 1991 was the first year of an organized, comprehensive census of burrowing owls in central California and any comparison of the 1991 data with the qualitatively different data from the previous years involves uncertainty. Nevertheless, the pre-1991 data can be viewed as a sample of known breeding locations from which qualified estimates of population change can be derived.

The limitations of the pre-1991 data can lead to three types of errors. First, some of the pre-1991 presumed breeding locations may not have been actual breeding locations but may have represented only wintering or transient birds. Second, because the pre-1991 data spanned five years, owls present at some of the locations in a given year may have been the same individuals recorded at different locations less than 2–3 km away in other years. Both of these errors will bias the pre-1991 number of breeding pairs toward the high side. On the other hand, the actual number of breeding pairs was not known for many of the pre-1991 breeding locations, especially in the Central Valley. This undoubtedly biased the pre-1991 number of breeding pairs toward the low side. The effects of these three biases may have tended to cancel each other.

The most likely error in the 1991 census data was that some owls were missed by the volunteer censusers. Although burrowing owls are generally quite easy to locate, they are cryptically colored and can be very difficult to see, especially if the grass around their nesting burrows is dense and tall. It is likely, therefore, that the actual number of breeding owls in the census area in 1991 could have been somewhat higher than the calculated estimate of 873 pairs. Similarly, the actual rate of decline in the number of pairs of burrowing owls between 1986–90 and 1991 could have been somewhat lower than the calculated estimate of 12–27%.

A final source of error could arise from misinterpretation of the 1991 census data, particularly if burrowing owls move their breeding locations from year to year by more than 2–3 km, such that some of the 55 new pairs of owls in some of the 24 new owl groups were actually previously-known owls that had disappeared from locations more than 2–3 km away. It is worth stressing, however, that only 64 groups totaling 318 pairs of breeding owls were found in 1991 in the adequately-censused portion of the entire census area, despite the fact that 2111 person-hours were spent searching 6195 km^2 for owls. Considering that as many as 83 groups totaling 362 pairs of breeding owls were previously known from this portion of the census area, the 1991 census data provides evidence for a decrease of at least 22.9% of the groups and 12.2% of the pairs of breeding owls during the 5-yr period 1986–91. This translates to a rate of decline for groups of about 4.6% per year and for pairs of about 2.4% per year.

Thus, despite the limitations of using pre-census owl data to estimate the decrease in the numbers of breeding owls in the census area and the uncertainties as to the exact accuracy of the 1991 census, it is obvious that burrowing owls have suffered substantial decreases in the numbers of both breeding groups and breeding pairs in central California in the past decade. This, coupled with estimates of a small total population size, portends a bleak future for the species in central California. Furthermore, anecdotal information on the status of burrowing owls elsewhere in California suggests that similar declines may be occurring in other regions as well. Clearly, a concerted attempt to identify the locations of most of the remaining breeding pairs of burrowing owls in California, along with a comprehensive monitoring program for the owls, is required to provide the detailed information necessary to design an effective recovery plan for the species in California.

ACKNOWLEDGMENTS

We extend our sincere appreciation to the more than 250 volunteer censusers who gave their time and energy to conduct the 1991 census. We also thank the area coordinators (names in parentheses), members, and directors of the following organizations for splendid cooperation in conducting this census: Redwood Regional Ornithological Society (Betty Burridge and Benjamin D. Parmeter), Marin Audubon Society (David Shuford), Sequoia Audubon Society (Peter Metropolis), Santa Cruz Bird Club (David Suddjian), Napa-Solano Audubon Society (Robin Leong), Golden Gate Audubon Society (Ann Dewart and Leora Feeney), Mount Diablo Audubon Society (James Lomax and Jean Richmond), Ohlone Audubon Society (Connie Nelson), Santa Clara Valley Audubon Society (Cecily Harris), Yolo Audubon Society (Joan Humphrey), Sacramento Audubon Society (Tim Manolis and Curt Sutliff), San Joaquin Audubon Society (David Yee), Stanislaus Audubon Society (Harold Reeve). We thank Lincoln Moses, Nadav Nur, and Lynne Stenzel for their help and guidance in sampling methods. We also thank J. Barclay and S. Terrill for many constructive comments on an earlier version of this paper. Finally, we thank the National Fish and Wildlife Foundation, Santa Clara Valley Audubon Society, Mr. and Mrs. B. Hammett, Pacific Gas and Electric Company, San Joaquin Audubon Society, Marin Audubon Society, Stanislaus Audubon Society, Mount Diablo Audubon Society, ARCO Foundation, Golden Gate Audubon Society, Los Angeles Audubon Society, Sacramento Audubon Society, San Bernardino Audubon Society, Monterey Peninsula Audubon Society, Santa Cruz Bird Club, Yolo Audubon Society, Ventura Audubon Society, Redwood Regional Ornithological Society, Fresno Audubon Society, Napa-Solano Audubon Society, Ohlone Audubon Society, Wintu Audubon Society, and more than 30 additional individual donors for financial support. This is Contribution No. 12 of The Institute for Bird Populations.

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Addenda

In order to provide additional estimates of population size and more rigorous estimates of population change, we duplicated the 1991 census of central California in both 1992 and 1993. Preliminary analyses of these data suggest that the number of breeding groups in the entire census area decreased by 16.7% from 1991–92 and remained constant from 1992–93, while the number of breeding pairs increased by 3.1% from 1991–92 and decreased by 5.2% from 1992–93. These data suggest that the number of breeding groups continued to decline substantially during the early 1990s while the number of breeding pairs declined only slightly during that time period, presumably because of excellent breeding success in 1991. In addition, the census area was expanded in 1992 and 1993 to include all of the remainder of the Sacramento and San Joaquin Valleys, the Coachella and Imperial Valleys, and the entire coastal slope of southern California from Monterey County to the Mexico border. Preliminary analyses of data from this expanded census area further confirmed the small and declining nature of burrowing owl populations throughout the remainder of the breeding range of the species in California.

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SEASONAL RECORDS OF THE BURROWING OWL IN MEXICO

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ABSTRACT.—I compiled data on 279 burrowing owls (*Speotyto cunicularia*) from 27 museums. The earliest burrowing owl specimens from Mexico are from 1840. Most individuals were collected from 1900–10. Sixty-three percent of specimens were from the non-breeding (wintering) season. The burrowing owl has a wide distribution in Mexico; it is located in 28 of 32 Mexican states. *S. cunicularia* has been the third most common owl collected in the country. Baja Peninsula has provided the most specimens; specimens are lacking for the southeastern region. The high number of individuals collected during the winter season suggests that Mexico is an important wintering area for burrowing owl populations.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *Mexico; distribution; breeding; museum specimens.*

Registros estacionales del Tecolote Zancón en México.

RESUMEN.—Se compiló un total de 279 datos del tecolote zancón (*Speotyto cunicularia*), provenientes de 27 museos. Las primeras colectas se registraron en 1840. La mayoría de los individuos se colectaron en la década de 1900–1910. El 63% de los especímenes se registraron en la temporada no reproductiva. El tecolote zancón presenta una amplia distribución en México, se localizó en 28 estados de la República Mexicana. *S. cunicularia* ha sido la tercer especie de búho más colectada en el país. La Península de Baja California contuvo el mayor número de especímenes y la región del sureste sobresalió por la falta de ellos. El elevado número de individuos presentes en la temporada no reproductiva, sugiere un incremento de las poblaciones del tecolote zancón en México, pudiendo ser este país una importante área de invernación.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) has a wide distribution in the western hemisphere, from southern Canada through South America, to Tierra del Fuego (A.O.U. 1983). Burrowing owls inhabit open lands and grasslands (Johnsgard 1988), nest in abandoned burrows, and exhibit both diurnal and nocturnal habits. In recent decades, the Canadian and U.S. burrowing owl populations have been decreasing because of several factors (James and Fox 1987, Weseman and Rowe 1987). This owl species has been listed in the Blue List since 1972 in the U.S.A. and classified as threatened in Canada (James and Ethier 1986). Principal reasons for the decline are loss of grassland habitats, use of insecticides, rodent poisoning programs, limited nest burrows, and shooting (Schmutz 1991).

Populations that breed in northern portions of the range winter south of the U.S.-Mexico border (James 1992). Although some banded northern burrowing owls have been recovered in Mexico and Central America, little is known about breeding and nonbreeding distributions in Mexico. In this paper, I discuss both historical and seasonal records and distribution of Mexican burrowing owls.

STUDY AREA AND METHODS

I obtained burrowing owl data from six national (Colección Ornitológica del Instituto de Biología, Colección Ornitológica de San Nicolás de Hidalgo-Univ. Michoacán, Escuela Nacional de Ciencias Biológicas, Instituto de Historia Natural de Chiapas, Instituto Nacional de Investigaciones sobre Recursos Bióticos, and Salón de las Aves de Saltillo Coahuila) and 21 foreign museums (British Museum, Bell Museum of Natural History, Carnegie Museum of Natural History, Cornell University Collection, Delaware Museum of Natural History, Museum of Natural History-Chicago, Forschungsinstitut und Naturmuseum Senckenberg, Harvard Museum of Comparative Zoology, Illinois State Museum Collection, Kansas University Collection, Los Angeles, California Museum of Natural History, Louisiana State University Museum of Zoology, Moore Laboratory of Zoology-Occidental College, Museum of Vertebrate Zoology-University of California Berkeley, National Museum Smithsonian Institute, Provincial Museum of Alberta, Rijksmuseum Van Natuvrlijke Historie-Leiden, Royal Ontario Museum, San Diego Museum of Natural History, Western Foundation

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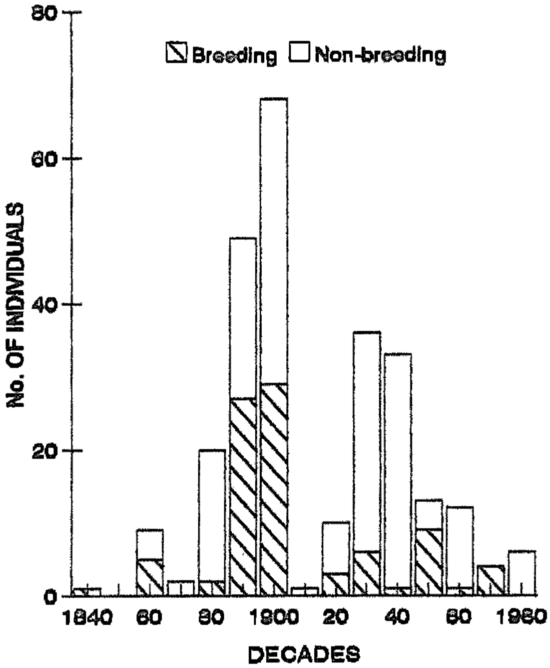

Figure 1. The number of burrowing owl specimens collected in México from 1840s through 1980s.

Vertebrate Zoology Collection, and Zoological Institute of the Academy of Sciences-Moscu).

Data were divided into two seasons: breeding (16 April–15 October) and nonbreeding (16 October–15 April) and analyzed by decades. Based on these data, I prepared a distribution map with breeding and nonbreeding ranges.

RESULTS

I compiled data on 279 burrowing owls. The earliest burrowing owl record found was collected in the 1840s. Most individuals were collected between 1900 and 1910 (Fig. 1), followed by 1890s (n = 49), 1930s (n = 36) and 1940s (n = 33). Sixty-three percent of the individuals were collected in the nonbreeding (wintering) season, and 37% were from the breeding season (Fig. 1). More than 80% collected since 1930 were from the nonbreeding (wintering) season, but recent decades (1960s, 70s and 80s) have produced only 8% of the total specimens.

Specimens were collected from 26 states (Fig. 2). Burrowing owls also have been recorded in Nuevo Leon (Friedman et al. 1950) and Durango (Rodríguez-Estrella pers. comm.), so I included these states in the distribution map. The Mexican state of Durango was included in the breeding range due to reports on nest-site selection by burrowing owls in that state (Rodríguez-Estrella and Ortega-Rubio 1992).

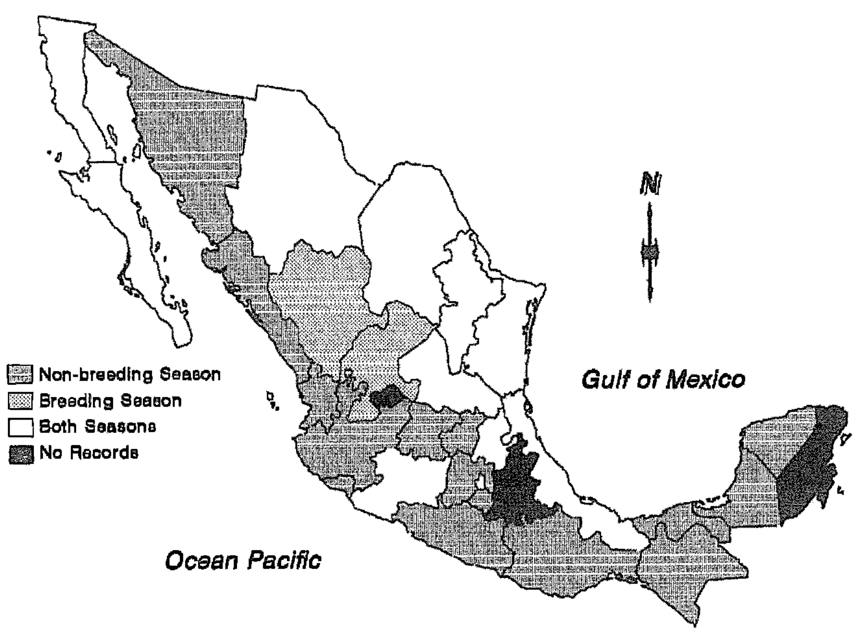

Figure 2. Burrowing owl distribution map showing breeding and nonbreeding areas in México.

Baja California has provided the most specimens (n = 61), followed by Colima (n = 36), Guerrero (n = 18), Sinaloa (n = 13) and Tamaulipas (n = 13). The other states provided from 1–11 specimens. The southeastern region stands out for a lack of information (Oaxaca [n = 5], Chiapas [n = 3], Tabasco [n = 11], Campeche [n = 1], Yucatán [n = 1], and no records for Quintana Roo). Although the state of Colima had 36 specimens, most of them were from Clarion Island (n = 27), in the Pacific Ocean. This land contains the subspecies *Speotyto cunicularia rostrata,* whereas the subspecies found on the mainland is *S. cunicularia hypugaea* (Ridgway 1914).

DISCUSSION

In Mexico the burrowing owl has a wide distribution, being recorded in 28 of the 32 states. It is the third most common owl species in the country, based on museum specimens (Enríquez 1990). The high number of specimens from the nonbreeding season suggests an increase of burrowing owl numbers during winter, probably due to the arrival of North American migrants. The increase in owl specimens from the winter season could also be accounted for by the arrival of ornithologists who migrate with the neotropical migrant birds. Nonetheless, existing records of the museum owl specimens may also depend on variables such as habitat, area, and time of day of capturing, as well as method and effort of capture by each collector.

The burrowing owl has been recorded in most Mexican states, but there are no records for the states of Aguascalientes, Puebla, Tlaxcala or Quintana Roo. Reasons for lack of specimens in these states are unknown, especially because there is no evidence of lack of suitable habitat.

Only breeding records were found in Durango and Zacatecas (Fig. 2). Excluding Michoacán and Baja California, only nonbreeding (wintering) data were located in the Pacific region, as well as in some central states and in the southeastern Gulf of Mexico (including the Yucatan Peninsula). Both breeding and nonbreeding records were found in northern Mexico, Baja California, and some states from the Gulf of Mexico.

In Mexico, breeding and wintering areas have not been well described. Also, the status of Mexican owl populations, as well as migration routes of northern populations, and the relative importance of factors affecting populations, continue to be unknown. I propose to begin an intensive program to record reports of burrowing owls. This program should establish a computer base center, and also facilitate plotting maps to determine the best conditions for burrowing owls. Both reports and maps will help identify preferred and/or priority use areas. In parallel with these efforts, a network should be established which involves researchers who are banding on both breeding and nonbreeding grounds, defining migration routes, determining resident populations and, perhaps, achieving other goals. Additionally, studies should be started on the ecology of owls at wintering areas establishing the effects of human activities and determining if this impact is contributing to the species' decline.

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ECOLOGY OF THE BURROWING OWL IN AGROSYSTEMS OF CENTRAL ARGENTINA

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ABSTRACT.—Studies on the ecology of the burrowing owl (*Speotyto cunicularia*) in agrosystems of central Argentina were conducted: (1) to record basic information on habitat use, food habits, differential predation on rodents, feeding strategy, and breeding biology; (2) to examine reproductive success and conservation needs; and (3) to examine the owl's regulatory effects on rodent populations. The burrowing owl is a generalist predator, and its diet strongly depends on the availability of alternative prey. It showed differential predation by species and size of rodents and a functional response to changes in the abundance of rodent populations. Nests are built in areas with relatively low disturbance. Reproductive success was as low as 0.3 fledged per brood. Brood size negatively affected the growth of chicks. Main mortality factors for eggs were agricultural practices and predation, and for chicks were illness and hunting. The low reproductive success of the burrowing owl suggests a declining population. Strategies for conservation should be initiated as soon as possible.

KEY WORDS: *burrowing owl; ecology;* Speotyto cunicularia; *Argentina; management; prey; agriculture; breeding biology; growth.*

Ecologia del tecolotito enano en agrosistemas de Argentina Central

RESUMEN.—Se realizaron estudios de la ecología de la lechucita vizcachera (*Speotyto cunicularia*) en agrosistemas de Argentina central con los objetivos de: (1) recopilar información básica acerca del uso del habitat, predación diferencial sobre roedores, estrategia alimentaria y biología reproductiva; (2) examinar el éxito reproductivo y las necesidades de conservación; y (3) examinar los efectos regulatorios de la predación sobre las poblaciones de roedores. La lechucita vizcacahera es un predador generalista cuya dieta depende de la disponibilidad de presas alternativas. Mostró una predación diferencial por especie y tamaño de roedores y una respuesta funcional a los cambios en la abundancia de roedores. Los nidos son contruidos en áreas con perturbaciones relativamente bajas. El éxito reproductivo fue muy bajo, 0.3 juveniles por puesta. El tamaño de la puesta afectó negativamente el crecimiento de los pichones. Las principales causas de mortalidad de huevos fueron las labores agrícolas y la predación, y de la mortalidad de pichones fueron las enfermedades y la caza. El bajo éxito reproductivo sugiere que esta población de lechucitas está declinando y que estrategias de conservación deberían iniciarse lo antes posible.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) may be found in almost all grassy plains of Argentina (Olrog 1978) and is common in agrosystems. Studies on the ecology of the burrowing owl in agrosystems of central Argentina started in the early 1980s. Initially, studies focused on burrowing owl predation on rodents because some rodent species were involved in human diseases and crop damage. The first step was to develop an accurate method to identify species, age, and sex of rodents found in pellets. After having this tool, studies dealt with diet and its seasonal changes, differential predation on rodent populations, and functional response. Later, evidence suggested a declining population of the burrowing owl, and subsequent studies focused on breeding biology and management. Here, I provide a review of the studies conducted by me on the ecology of the burrowing owl in agrosystems of central Argentina, setting priorities for future research.

STUDY AREA

Studies were conducted approximately 100 km northwest of Buenos Aires city, province of Buenos Aires, Ar-

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gentina (34°18'S, 59°14'W) during 1982–88. The study area was located in the Pampa region in the east central part of the country. The region shows moderate weather conditions, with a mean daily temperature of 9.8°C in winter and 22.5°C in summer, and an annual mean precipitation of 946 mm varying from 130 mm in winter to 306 mm in summer (INTA 1972). The area was originally a natural prairie. Having highly productive soils, it was subsequently and completely used for agrarian activities since the beginning of the nineteenth century. Today, the northern portion of the region, where these studies were conducted, is devoted mostly to farming (especially cereal crops) with a few areas used for ranching. Three main kinds of habitat may be distinguished: (1) cultivated fields that experience strong perturbations due to farming; (2) fields with natural grass used for grazing cattle; and (3) margins of cultivated fields, extremely narrow corridors that show relatively low disturbance.

Food Habits. The diet of the burrowing owl and its seasonal changes were studied in detail for one year (Bellocq 1988a). A total of 1176 pellets collected during 1982–85 were qualitatively analyzed to identify prey items to the level of Order. Rodent species were quantified in the content of 609 pellets (140 pellets collected in spring, 83 in summer, 231 in fall, and 150 in winter) following Bellocq and Kravetz (1983). A detailed quantification of the diet was conducted for a subsample of 128 pellets (26 collected in spring, 26 in summer, 44 in fall, and 32 in winter). Data on the number and biomass of prey consumed were analyzed by season.

Differential Predation on Rodents. The consumption and abundance of rodent species, size, and sex were compared to determine whether the burrowing owl preyed differentially on rodent populations (Bellocq 1987, Bellocq and Kravetz in press). Relative abundance of rodent species, size, and sex was estimated by livetrapping. Eighteen Sherman trap lines were set in fields and margins (total effort-1400 trap nights). Traps operated from 1–7 June 1984, when rodents were most abundant in the field (for details on field methods see Bellocq 1987). Captured rodents were identified and classified into three groups (juveniles, sub-adults and adults) according to their mass (Bellocq and Kravetz 1994). Consumption of rodents by the burrowing owl was estimated by pellet analysis (113 and 164 pellets to study predation by rodent species and by size-sex, respectively). Species, size categories, and sex were identified from pellets using molars and pelvis (Bellocq and Kravetz 1983). Identifications, especially sex, were not possible in some cases because the molars were absent or the pelvis broken. Regressions between body mass and tooth wear allowed prediction of rodents mass found in pellets (Bellocq 1988b). Manly's alpha (Chesson 1978) was used to obtain food preference indices.

Functional Response. Abundance of rodents was estimated monthly by livetrapping in approximately 100 ha during 1984. Consumption of rodents by burrowing owls was also estimated monthly by analyzing pellets collected in the same area as the trapping was conducted (see Bellocq 1988b for details on field methods). Regression analysis was performed between the number of rodents per pellet and the abundance of rodents in the field.

Effects of Agricultural Practices on Rodent Predation by Burrowing Owls. The effects of harvest and plowing

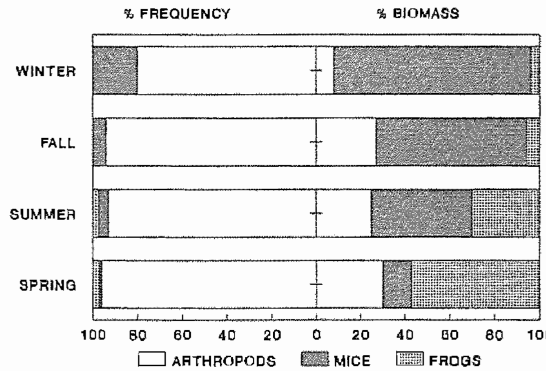

Figure 1. Percentage frequency of the number of prey items (N = 791) and percent biomass of arthropods, mice, and frogs found in pellets of burrowing owls, and their seasonal changes in agrosystems of central Argentina.

on rodent predation by the burrowing owl were examined as part of a project to assess the effects of agricultural practices on rodent populations (de Villafañe et al. 1988). Abundance of rodents was estimated using a grid of Sherman traps in a cornfield during four periods, pre- and post-harvest and pre- and post-plowing. Consumption of rodents was estimated by analyzing pellets of burrowing owls whose burrows were closer than 500 m from the experimental cornfield during the same periods as the trapping was conducted.

Breeding Biology. Some aspects of the breeding biology of the burrowing owl were observed during 1983–87 and recorded in 1988 (Bellocq 1993). Seven nests with eggs were followed during the breeding season, and the brood size, reproductive success, and mortality factors were recorded for each nest. Chicks were weighed every 2–5 days and growing curves were constructed. Seven artificial nest burrows (Collins and Landry 1977) were set in margins of fields grazed by cattle and checked weekly for one year.

RESULTS

Diet. The burrowing owl was a generalist predator in agrosystems of central Argentina (Bellocq 1988a). Its diet contained a large number of different prey including arthropods (beetles, grasshoppers, spiders, etc.), small mammals (mice, bats, etc.), and frogs, snails, snakes, birds, etc. Most of these prey, however, occurred only occasionally in the diet. The main food consisted of arthropods, mice, and frogs. In terms of the number of prey items consumed year round (total number of prey 791 in 128 pellets), arthropods represented 91% of the diet, rodents 8%, and frogs 1% (Fig. 1). In terms of biomass, however, rodents and frogs were more important than arthropods. Based on a total

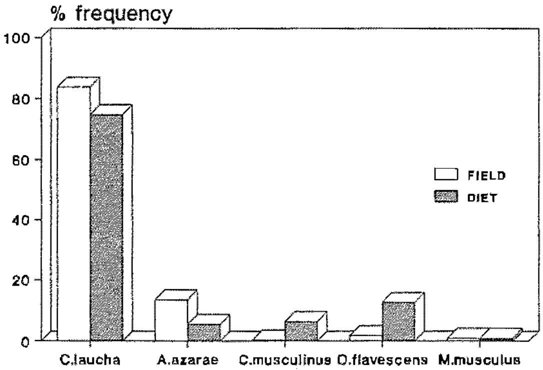

Figure 2. Percentage frequency of the number of rodents (N = 111) by species in the field and in the diet of the burrowing owl in agrosystems of central Argentina.

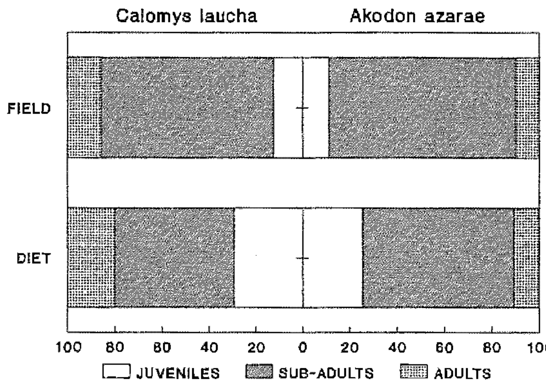

Figure 3. Percentage frequency of the number of *Calomys laucha* (N = 116) and *Akodon azarae* (N = 47) by size categories in the field and in the diet of the burrowing owl in agrosystems of central Argentina.

of 343 rodents identified in 609 pellets, *Calomys laucha* was the most common species (67%) followed by *Akodon azarae* (12%), *Calomys musculinus* (10%), *Oligoryzomys flavescens* (10%), and *Mus musculus* (1%).

The proportion of food types in the diet showed seasonal changes. The number of rodents per pellet, e.g., increased from 0.1 in the spring to 1.1 in the winter while the number of frogs per pellet dropped from 0.2 in the spring to 0.02 in the winter. This showed a shift in the diet typical of generalist predators.

Differential Predation on Rodents. Burrowing owls preyed preferentially on rodent species (Bellocq 1987). The number of individuals of different rodent species found in pellets (total number of identified individuals was 111 in 113 pellets) was independent of their abundance in the field (X^2 = 244.8, $P < 0.001$). *Oligoryzomys flavescens* and *C. musculinus* were the preferred species; whereas *A. azarae* was eaten in a lower proportion than expected based on trap captures (Fig. 2). *Calomys laucha* was taken in a similar proportion to what was available in the field.

The burrowing owl showed differential predation on rodents by size categories (Bellocq and Kravetz 1994). The observed frequencies of size categories of rodents in the diet (total 116 *C. laucha* and 47 *A. azarae* found in 164 pellets) were different from the expected based on trap captures (X^2 = 36.9, $P < 0.001$ and X^2 = 9.2, $P < 0.02$, for *C. laucha* and *A. azarae*, respectively). Food preference indices showed that burrowing owls preyed on medium-sized rodents in a lower proportion than expected according to their relative abundance. Juvenile rodents were eaten more than expected while large-sized adults were taken as expected (Fig. 3). The analysis of predation by sex (based on 27 *C. laucha* identified in 164 pellets) showed burrowing owls took females and males *C. laucha* according to the estimated sex ratio (X^2 = 0.6, $P > 0.1$) (Bellocq and Kravetz in press).

Functional Response. Analysis of the availability and consumption of rodents during one year showed that burrowing owls responded functionally to the abundance of rodents in agrosystems of central Argentina (Fig. 4) (Bellocq 1988b). The mean number of rodents per pellet depends on the abundance of rodents (R^2 = 0.747, F = 20.53, $P < 0.005$).

Effects of Agricultural Practices. Results showed that harvest and plowing increased the impact of owl predation on rodents (de Villafañe et al. 1988). After harvest, the mean number of rodents per pellet increased 10 times while the abundance of rodents was similar in the pre- and post-harvest periods (Table 1). The number of rodents per pellet was similar during the pre- and post-plowing periods whereas the abundance of rodents in the field decreased after plowing.

Breeding Biology. Nests were found in areas with relatively low disturbance. The agricultural systems on this land include rotations in seeding which result in some fields laying fallow from several months to a few years. Most nests of burrowing owls were found in these kinds of fields, in small areas with short grass around farms, and in mar-

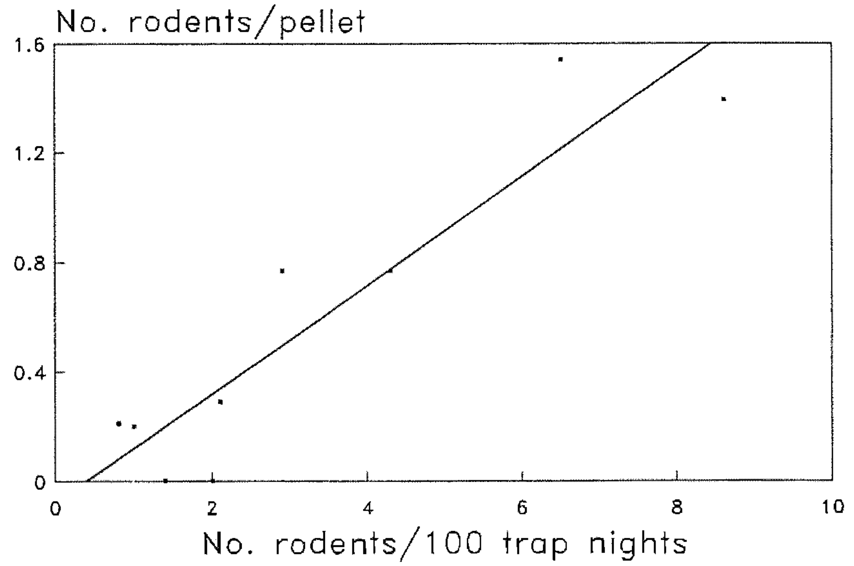

Figure 4. Functional response of the burrowing owl to changes in the abundance of rodents in agrosystems of central Argentina.

gins. In general, burrows were located close to fence posts. Nests were placed at the terminal portion of the burrows and their floors were covered with dry cattle dung. Artificial nest burrows were not colonized by burrowing owls.

Eggs were laid in mid-spring (October–November), followed by hatching in mid-November to early December (Bellocq 1993). The average clutch size was 4.8 ± 1.2 eggs (mean ± 1 SD), and the mean number of hatchlings per nest was 3.5 ± 2.4. Reproductive success was as low as 0.3 fledged per brood. Of the total number of eggs (N = 32), 66% of them hatched and only 10% of the total number of hatchlings (N = 21) survived to fledge.

Table 1. Abundance of rodents and number of rodents per pellet during the pre- and post-harvest and pre- and post-plowing periods in a cornfield.

	No. rodents/ 100 Trapnights	No. rodents/ Pellet
Harvest		
pre-treatment	14	0.04
post-treatment	12	0.41
Plowing		
pre-treatment	8	0.80
post-treatment	1	0.81

Main mortality factors of eggs were agricultural practices and predation (presumably by marsupials), and main causes of chick mortality were illness and hunting.

Brood size negatively affected the growth of chicks (Bellocq 1993). Although hatching was generally synchronized, older chicks grew faster than younger chicks in the same clutch (Fig. 5). Similarly, chicks belonging to smaller broods grew faster than chicks belonging to larger clutch sizes (F = 4.74; $P < 0.05$ for broods of 2, 3, 4, and 5 chicks 8-d-old, and t = 4.18, $P < 0.01$ for broods of 2 and

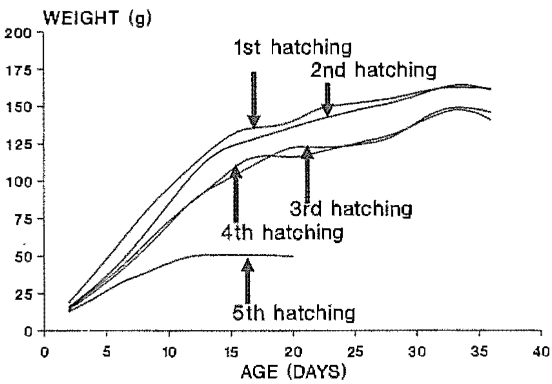

Figure 5. Growth curves of five burrowing owl chicks belonging to the same brood.

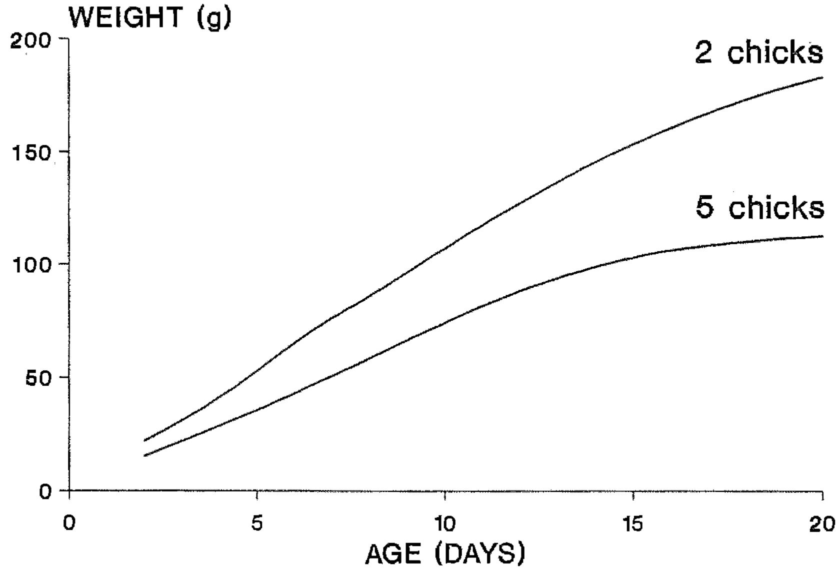

Figure 6. Mean growth curves of chicks belonging to broods of two and five chicks.

5 chicks 20-d-old, respectively) (Fig. 6). Chicks weighed 9.5 g at 1 day and reached 170 g in 20 days. They fed mainly on insects and frogs, and started to fly at approximately 40–50 days of age.

DISCUSSION

The biomass provided by different types of food varied seasonally. Rodents were the main source of food responsible for the winter survival of burrowing owls. Although most of the small mammals found in pellets were mice, the burrowing owl is able to prey on larger mammals in this area, like *Ctenomys talarum* and *Cavia pamparum* (Pearson et al. 1968, de Villafañe et al. 1988). During the breeding season, frogs were the primary food. Because brood size had a negative influence on the growing of chicks, food supplement might help to improve body condition and increase survival of chicks.

The burrowing owl showed an opportunistic feeding behavior. Consumption of rodents increased, whereas consumption of frogs decreased from spring to winter, following changes in the abundance of both kinds of prey in the fields. The burrowing owl's choice of juvenile rodents may be explained by the high vulnerability of juveniles, supporting the argument of an opportunistic feeding behavior. Selection of rodents by size categories may be linked with differences in rodent vulnerability by age or social hierarchy. Generally, adult rodents (socially dominant) display territorial behavior that decreases predation risk through increasing knowledge of the habitat and the ability to escape from predators (Metzgar 1967). Thus, juvenile rodents would be more vulnerable to predation than adults.

Burrowing owl predation on rodents increased as the abundance of rodents increased. This suggests that the burrowing owl might contribute to the regulation of rodent populations. It is a generalist predator and presumably resident all year round. Moreover, the environment provides a good supply of alternative prey. Although studies on dispersal and migration were not conducted in this area, observations showed that the burrowing owls may be seen all year round in agrosystems of central Argentina. However, numerical response to the abundance of rodents may occur when rodents increase some years. Increasing the numbers of burrowing owls may result in increased predation on rodents and contribute to the biological control of rodents involved in human diseases and crop damage.

Artificial nest burrows were not colonized showing that the availability of nesting sites is unlikely a limiting factor of burrowing owl population growth in agrosystems of central Argentina. However, availability of suitable nesting habitat and quality of nesting sites may be negatively affecting reproductive success. Burrowing owl nests are mainly found in fields with natural grasses that are uncommon in the northern part of the Pampa region. Leaving small patches of natural grass surrounding croplands would provide additional nesting habitat. When plowing, a small area surrounding the existing nests could be left untouched. Burrows used for nesting are frequently short (the shortest found was about 30 cm long) which may increase vulnerability to predation and hunting. Likely because of this, and in contrast with most North American observations, burrowing owls in the study area leave their nests when humans or animals approach the nest (they only remain in the nest when eggs are close to hatching or chicks are younger than approximately 10-d-old). Alternatives to improve quality of nest sites should be analyzed and implemented. For instance, nest quality was the primary cause of mortality of barn owl (*Tyto alba*) chicks in the study area (chicks fell down from human constructions). Productivity of the barn owl, however, was improved 50% by setting artificial nest boxes (Bellocq and Kravetz 1993).

In agrosystems of Argentina, future research should be oriented toward long-term studies (population dynamics, reproductive success, key mortality factors) and development of management strategies. The low reproductive success documented here suggests that this population may be declining drastically, and that strategies for conservation should be put in place as soon as possible. Some suggestions on habitat management were provided above, but regulations should be developed together with educational programs.

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GENETICS AND BREEDING BIOLOGY

J. Raptor Res. Report 9:58–63

CHARACTERIZATION OF POPULATION AND FAMILY GENETICS OF THE BURROWING OWL BY DNA FINGERPRINTING WITH pV47-2

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ABSTRACT.—Genetic attributes of the burrowing owl (*Speotyto cunicularia*) were revealed by DNA fingerprinting with the minisatellite probe pV47-2. I report here on DNA fingerprint variability, fingerprint inheritance and rate of mutation, and population substructuring. Each genetic profile comprised an average of 28.9 highly variable, somatically stable Mendelian markers, and contained single-locus, as well as multilocus, banding patterns, depending on hybridization stringency. Individual fingerprint specificity was minimally 8.4×10^{-17}, with an estimated mutation rate of 0.005. Allelic and genotypic frequencies at the pV47-2 locus indicated genetic substructuring within a pool of several geographically separated burrowing owl populations from western North America, and within a pool of populations from California, as well as inbreeding in an intensively-studied California burrowing owl population. These results suggest that nonrandom breeding and population subdivision in this species may be occurring at very fine spatial scales, levels of inbreeding may be elevated, and burrowing owl genetic effective population size may be small. If local populations are genetically and demographically isolated from one another, local extinctions may be exacerbated, and recolonization from extant burrowing owl populations will be less likely.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *DNA fingerprinting, avian genetics.*

Caracterizacion genetica de poblacion y familiar del tecolotito enanon usando huellas de ADN con pV47-2

RESUMEN.—Atributos geneticos del tecolotito enano (*Speotyto cunicularia*) se evaluaron con huellas de ADN con el minisatelite pV47-2. Aqui reporto la varibilidad de huellas de ADN en la herencia de huellas y el grado de mutacion y en la subsestructura de la poblacion. Cada perfil genetico comprendio un promedio de 28.9 marcadores Mendelianos somatico estables con alta variabilidad y contenian patrones de bandas con sitios unicos y sitios multiples, dependiendo en el grado de hibridacion. Especificidad de huellas individuales fue minima 8.4×10^{-17}, con una taza de mutacion de 0.005. Frequencias alelicas y genotipicas en el sitio pV47-2 indico subestructura genetica dentro del caudal de varias poblaciones de tecolotito enano separadas geograficamente del resto de Norte America y dentro de un caudal de California asi como intracruzamiento en una poblacion intensamente estudiada en California. Estos resultados sugieren que la repoduccion no al azar y subdivision de la poblacion esta ocurriendo a escala espacial muy fina, que los niveles de intracruzamiento pueden ser elevados y que la poblacion geneticamente efectiva del tecolotito enano puede ser chica. Si poblaciones locales estan geneticamente y demograficamente aisladas de las demas, extinciones locales se pueden exagerar y recolonizacion de poblaciones existentes es poco probable.

[Traducción de Filepe Chavez-Ramirez]

A major goal of my research (Johnson 1996a,b) is to characterize genetic and demographic parameters in order to examine the basis of population dynamics, population structure, and breeding systems in the social fossorial burrowing owl (*Speotyto cunicularia*). Because burrowing owls conduct a substantial portion of critical behaviors underground or at night, comprehensive direct observations are often not feasible. Consequently, the

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first step in these studies was to develop genetic techniques that would reveal in detail the mating systems, genealogies, and patterns of reproductive success in wild burrowing owl populations.

Because the interpretation and utility of hypervariable genetic markers depends on assumptions of Mendelian inheritance, somatic stability, linkage equilibrium, and a high degree of polymorphism, and because these assumptions may not always hold (Burke and Bruford 1987, Jeffreys and Morton 1987, Jeffreys et al. 1987), empirical tests need to be made, where possible, of markers that result from various combinations of species, DNA probe, and analytical conditions (see Epplen 1991). I report here on pV47-2 fingerprint variability in burrowing owls, and on fingerprint inheritance, rate of mutation, and population substructuring.

METHODS

I analyzed DNA from three subgroups of North American burrowing owls. I collected the largest number of blood samples (from 18 adults and 49 young) from a wild population of burrowing owls in Davis, California, in 1987–88, during the fieldwork described by Johnson (1996a,b). In 1987 I obtained another California sample from a group of wild owls (10 individuals, including two putative sibships) being held by the Santa Clara Humane Society prior to local translocation in Santa Clara County, California. Two other burrowing owl families (five individuals in each) from a Canadian captive-breeding project (Owl Rehabilitation Research Foundation, Vineland, Ontario) composed the third sample, collected in 1990. This was the only group available to me in which each adult pair had been reproductively isolated from others, ensuring exclusive parentage. The captive adults used in these controlled matings came originally from Manitoba, Idaho, and Wyoming, locations too disparate to be combined for a thorough analysis of population genetic structure. However, the samples were useful for the study of the inheritance of DNA fingerprint patterns, unconfounded by unknown matings.

Nuclear DNA was isolated by standard protocols (Maniatis et al. 1982, Ausubel et al. 1987) from blood collected from each burrowing owl by brachial venipuncture. The DNA was cleaved with HinfI and size-fractionated in 0.6% agarose gels run at 30 V for 44 hrs in recirculating TBE. Hybridization with minisatellite probe pV47-2 (provided by J. Longmire, Los Alamos National Laboratory; Longmire et al. 1990) was generally performed as described by Westneat et al. (1988) for M13 bacteriophage probes. All blots were washed at low stringency in 2 × SSC/0.1% SDS, once for 15 min at room temperature and once for 15 min at 60°C. After exposure to Kodak X-Omat AR film for 1–3 d, the blots were subsequently washed at high stringency with 0.5 × SSC/0.1% SDS at 60°C.

DNA fingerprint analysis was automated by high-resolution transmissive camera scanning using a Bio Image digitizing system consisting of a Sun/Sparc2 Workstation, Visage software, and a Megaplus VME-interfaced camera capable of converting an autoradiograph into a 1024 × 1024 pixel image. In the images used for this analysis, resolution was ultimately limited by the fact that one camera pixel unit corresponded to about 100 bp at high molecular weights (e.g., 20 kb) and to about 5 bp at 2.3 kb.

To estimate the frequency of DNA fragments and "alleles," I collapsed the distribution of band sizes into larger size categories, or bins (see Budowle et al. 1991 for the general procedure). I used three different binning strategies (see Table 1), based on (1) variation among replicates on different gels, (2) differences in the sizes of homologous bands across one gel (calculated from the known pedigrees), and (3) resolution of the digitized images.

Table 1. Binning strategies for determination of fragment and allele frequencies.

	BIN SIZES (BP) BASED ON		
MW RANGE (BP)	VARIATION AMONG GELS	VARIATION WITHIN GELS	IMAGE RESOLUTION (PIXELS)
15870–23130	400	230	100
9416–15870	285	140	60
6682–9416	169	70	40
4361–6682	120	45	15
2322–4361	76	28	15

RESULTS

Inheritance. DNA fingerprints were inherited as somatically stable Mendelian markers. Ninety-one clearly resolved unique parental bands were scored in the two captive-bred owl families. Those fragments known to be inherited by only some progeny were transmitted on average to about half of the offspring of each parent ($\bar{x}$ = 53.7% ± 2.83% SE), generally in agreement with a 1:1 segregation ratio. I compared the number of offspring that received each unique parental fragment to the expected binomial distribution, assuming 50% transmission. The data for all adults combined were consistent with binomial expectations (*G*-test with Williams' correction, $P < 0.006$).

Mutation. The mutation rate per locus per generation was estimated to be 0.005. In DNA fingerprints from the two captive burrowing owl families with known pedigrees, only one of 212 offspring bands was novel, in that it did not correspond to fragments detected in either of its parents.

Multilocus Fingerprints. Multilocus DNA fingerprints were highly polymorphic. Hybridization of burrowing owl DNA with pV47-2 revealed a diverse array of fragments in the molecular weight range of 1.5–25.0 kb in all samples. At low stringency an average of 28.9 fingerprint bands (±5.30 SD) could be resolved per individual (N = 87). In the captive burrowing owl families, an average of 62% of parental bands were transmitted to some offspring. There was no single fingerprint band size, among the 462 resolved by the smallest binning scheme (absolute image resolution), that appeared in all individuals sampled. Even when I grouped bands in a manner which accommodated maximum among-gel error, the frequency of a few size categories (each of which might actually have represented one fragment size) approached , but did not exceed, 76%.

Locus-Specific Bands. When the blots were washed at high stringency, only one or two bands (in the homozygous or heterozygous case, respectively) remained in each lane at positions between 16 and 23 kb. This pattern can be most parsimoniously interpreted as being due to a single locus possessing a large number of alleles. Based on bin (allele) sizes that were derived from variation among sample replicates on different gels, at least 15 alleles exist at this locus and the mean frequency of an allele is 0.1138 (±0.0856 SD). Alternatively, using bin sizes based on absolute image resolution suggests up to 50 alleles at this locus, with a mean allele frequency of 0.0392 (±0.0321 SD).

Fingerprint Individuality. Individual specificity of DNA fingerprints is based on the premise that fragments having the same mobility (hence the same size) in different individuals represent the same allele (Geursen 1990). Under this simplifying assumption, the frequencies of fragment occurrence in hypervariable multilocus fingerprints are analogous to multilocus allele frequencies. I calculated the estimated average probability p, that an allele present in one burrowing owl is also present in another, from the proportion of individuals possessing a fragment in a particular bin size category (Jeffreys et al. 1985b, Geursen 1990, Kirby 1990). Using the two most extreme binning criteria, I was able to derive a range of values for p from the DNA fingerprints of 27 presumably unrelated burrowing owls (adults, all populations). Binning based on variation among gels resulted in a minimum of 102 bins (alleles), with a mean frequency of 0.2778 (±0.1930 SD) per allele in the population, whereas binning based on image resolution suggests at least 531 bins, with frequency averaging 0.0625 (±0.0510 SD). I calculated a range for the probability p^n, that two random burrowing owls could share a DNA fingerprint, where n is 28.9, the average number of bands per individual. The chance of two unrelated burrowing owls having the same pV47-2-detected multilocus fingerprint therefore appears to lie between 8.4×10^{-17} and 1.6×10^{-35}.

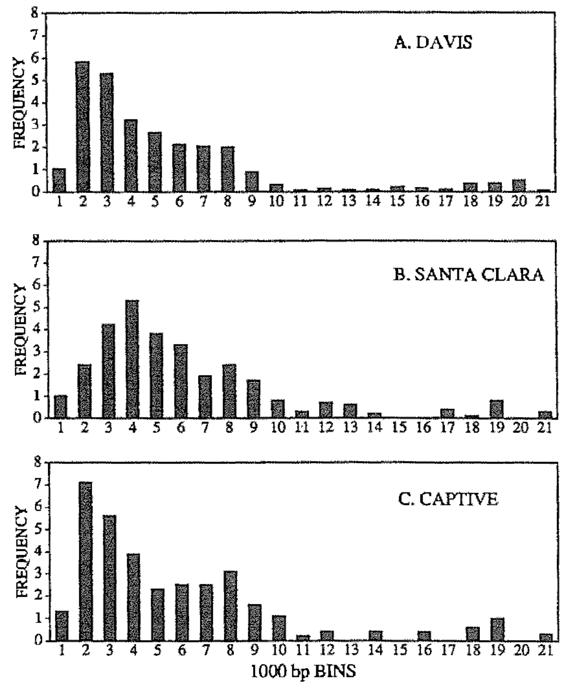

Figure 1. Frequency distributions of multilocus DNA fragments from individuals sampled from three geographically separated burrowing owl populations (A. Davis, CA: n = 67; B. Santa Clara, CA: n = 10; C. Captive: n = 10). Bands (putative alleles) were combined in 1000 bp bins. Most bins were represented in all samples; bins 15 and 20 were unique to the Davis population.

Population Comparisons. Coarse size distributions of multilocus fragments in the Davis, Santa Clara, and Canadian captive-breeding ("Captive") populations are shown in Fig. 1, where bands have been combined in 1000 bp bins. All three distributions are bimodal. Binned fragments in the Santa Clara and Captive samples (Fig. 1B,C) fall within the size range of alleles detected in the Davis sample (Fig. 1A). Most bins are represented in all groups, and the only bins unique to a sample were bins 15 and 20, which are only represented in the Davis sample.

At the single locus I analyzed sample substructuring by the method of Chakraborty et al. (1991),

Table 2. Test for Hardy-Weinberg equilibrium of single-locus genotype frequencies detected by the pV47-2 probe in burrowing owls.

	SOURCE POPULATION									
	ALL		CAPTIVE		CALIF.		DAVIS		S. CLARA	
	OBS	EXP	OBS	EXP	OBS	EXP	OBS	EXP	OBS	EXP
Number of										
heterozygotes	67	77.5	9	8.2	58	66.5	52	58.4	6	7.1
homozygotes	20	9.5	1	1.8	19	10.5	15	8.6	4	2.9
P[a]	$<.001$		>0.5		$<.01$		$<.05$		>0.5	

[a] Based on the method of Chakraborty et al. (1991). Chi-square, 1 df; test results are given for homozygotes only; differences between observed and expected heterozygote frequencies are not statistically significant.

which uses the Chi-square distribution to test for an excess of homozygotes. I compared the observed proportions of homozygotes and heterozygotes of all types to those expected for a randomly breeding population at Hardy-Weinberg equilibrium. Table 2 summarizes these results for the combined samples (all groups) and for the successively smaller population units. This analysis suggests that the pool of all populations was genetically substructured, as was the collective California sample. Moreover, there was some evidence of nonrandom breeding, even in the Davis sample alone. The only groups that conformed to Hardy-Weinberg expectations were the samples from Santa Clara (which included one large sibship) and the captive-breeding project, both of which should exhibit Hardy-Weinberg ratios because they were limited to defined matings.

DISCUSSION

DNA fingerprints detected in the burrowing owl with the pV47-2 probe have single-locus, as well as multilocus, characteristics. This combination increases their value as markers for fine-scale population studies. Depending on the hybridization conditions used with DNA from this species, the pV47-2 probe alternatively has (1) the high resolving power typical of most minisatellite probes, or (2) the clear allelism and ease of scorability of a simple single locus with alleles characterized by a variable number of tandem repeats (see Gibbs et al. 1990). Similar cases of single locus probes loosely hybridizing at low stringency to alleles at many autosomal loci have been reported for birds (Gyllensten et al. 1989), as well as for other organisms (Higgs et al. 1986, Jarman et al. 1986, Nakamura et al. 1987, Ali and Wallace 1988, Fowler et al. 1988). Although the multilocus fingerprints of burrowing owls, like those described in the above studies, lack some precision in unambiguously resolving alleles because of some base-pair mismatch, the fingerprints are composed of highly variable Mendelian markers. Their major drawback, that DNA fragments cannot be attributed to particular loci, is offset by the ability, at the pV47-2 single locus, to analyze bands as traditional Mendelian, albeit hypervariable, alleles.

The use of DNA fingerprints as genetic population markers is also contingent on somatic stability and a relatively low rate of spontaneous gametic mutation. The estimated mutation rate per locus per generation for the burrowing owl (0.005) was within the range of values that have been reported for other birds, as well as for humans (0.003–0.05; Jeffreys et al. 1985a, Wetton et al. 1987, Rabenold et al. 1990), and would not invalidate use of the fingerprints for parentage determinations. Because the burrowing owl DNA came from red cells in peripheral blood, each sample represented an individual's entire erythropoietic system (see Longmire et al. 1988), indicating at least regionalized somatic stability.

Although I did not find significant deviation among the three burrowing owl population samples in fragment distribution or frequency, there is contradictory evidence for substructuring in the only wild population comprehensively sampled (i.e., Davis, California), based on the total number of homozygotes observed. That Hardy-Weinberg expectations were met in the Santa Clara and the captive breeding groups is hardly surprising, as such a small sample of parents virtually ensures Hardy-Weinberg equilibrium (i.e., the breeding system is reduced to just a few Mendelian crosses).

Nevertheless, these data suggest that selection is not acting to alter allelic frequencies at loci revealed in the DNA fingerprints.

If the data from the Davis sample can be generalized to other populations of burrowing owls, nonrandom breeding and subdivision may be occurring on very fine spatial scales (e.g., on the order of hundreds of meters). If the population is strongly subdivided, there may be elevated levels of inbreeding, and genetic effective population size may be small. In fact, estimates of relatedness based on DNA fingerprint similarity in the Davis burrowing owl population (see Johnson 1996b) indicate that the owls are experiencing inbreeding as a result of small deme size rather than nonrandom mating. In addition, if local populations are genetically and demographically isolated from one another, local extinctions may be exacerbated, and recolonization from extant populations may be less likely.

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REPRODUCTIVE SUCCESS, RELATEDNESS, AND MATING PATTERNS OF COLONIAL BURROWING OWLS

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ABSTRACT.—DNA fingerprinting was used to characterize patterns of mating, genealogies, and reproductive success in a wild population of burrowing owls (*Speotyto cunicularia*) in Davis, California. The data revealed important discrepancies between patterns suggested by inference and those documented by direct genetic measurement. DNA fingerprints showed that in 20% of the cases, genetically determined parent-offspring relationships and those suggested by direct behavioral observations disagreed. Differences were due to nestling movements and brood mixing, extra-pair fertilizations (which resulted in at least 5–10% of offspring), polygamy, and possibly intraspecific brood parasitism. These previously undocumented aspects of burrowing owl mating biology collectively resulted in alloparenting by 37% of the adult owls. Most of these behaviors can be expected to enhance within-population genetic heterogeneity and contribute to variation in individual reproductive success.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *DNA fingerprinting; extra-pair copulation; reproductive success; mating patterns.*

Exito reproductivo, parentesco y patrones de apareo de colonias del tecolotito enano

RESUMEN.—Huellas de ADN se usaron para caracterizar patrones de apareo, genealogia y exito reproductivo de poblaciones silvestres de tecolotito enano (*Speotyto cunicularia*) en Davis, California. Los datos mostraron importantes desacuerdos entre patrones sugeridos por inferencia y esos documentados por medidas geneticas directas. Huellas de ADN mostraron que en 20% de los casos determinados geneticamente y esos sugeridos por observaciones de conducta directa no estaban en acuerdo con respecto a parentescos padre-hijo. Las diferencias se debieron a movimiento de volantones y mezcla de nidadas, fertilizacion por otros individuos-no la pareja (que resultaron en cuando menos 5–10% de hijos), poligamia y posible parasitismo de nidada intraespecifico. Estos aspectos no documentados previamente de la biologia reproductiva del tecolotito enano collectivamente resultaron en allopadrazgo por 37% de tecolotes adultos. Se puede esperar que la mayoria de estas conductas realzen la hetorogeniedad genetica de la poblacion y contribuyan a la variacion en exito reproductivo individual.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) resembles most monogamous birds and most other owls in that both parents care for offspring. In other ways, however, it is unique. Although it is primarily a nocturnal predator, the burrowing owl is diurnally active, especially during the breeding season. It roosts and nests in subterranean burrows that are usually excavated by other animals, particularly mammals, that inhabit structurally simple grassland and desert habitats (Coulombe 1971, Martin 1973, Zarn 1974, Wedgwood 1976). Throughout extensive regions of its distribution, the burrowing owl nests in aggregations (often referred to as colonies), in part as a result of patchy dispersion of host burrows. In such instances, pairs can be densely distributed, numbering from several to tens in just a few hectares. At such densities, they are easily within visual range of each other during the months of breeding. Burrowing owl nestlings are brooded underground and emerge before they can fly. Even in this early prefledging stage (analogous to the "brancher" phase of arboreal owl development), the young owls range extensively on foot.

For other birds, high local densities and mobile young increase the risk that parents will care for foster offspring because they promote clandestine copulations with neighbors, egg-dumping by nearby females, and mixing or merging of broods

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(Gladstone 1979, Mock 1983, Westneat et al. 1990). Indirect behavioral evidence suggests that all of these behaviors are consequences of burrowing owl aggregation. For example, behavioral evidence for extra-pair copulations has been recorded for at least two other burrowing owl populations (Haug 1985, S. Honeyman and E. Musso, unpubl. data). In preliminary observations of color-marked burrowing owls, I saw attempts by both sexes to transfer care of offspring to individuals outside the pairbond. These behaviors included male solicitation of copulation with nearest-neighbor females and visits by females to burrows containing nests not their own. In addition, in each of two years, one nest in this burrowing owl population was defended and provisioned by three adults, further confounding my ability to infer parentage from behavioral observations and to determine relative reproductive contributions. Finally, brood mixing occurred regularly, making it difficult to estimate reproductive rates and intrasexual reproductive variance.

A number of recent studies that have used genetic tools to examine mating patterns and individual reproductive success in wild populations has confirmed that behavioral observations do not accurately reflect individual fitness in other social birds (Burke et al. 1989, Morton et al. 1990, Rabenold et al. 1990, Westneat et al. 1990). For this reason, I evaluated whether behavioral assessments of reproductive performance and mating system agreed with estimates obtained by genetic analysis for a highly social resident aggregation of burrowing owls. In addition, I sought to estimate the degree of genetic relatedness in this owl population in order to begin to understand genetic patterns that contribute to, and result from, burrowing owl group living.

METHODS

Study Population. I studied a wild population of burrowing owls in Davis, California, during four breeding seasons (April–September) in 1985–88. The population occupied remnants of nonnative annual grassland in a 150-ha human-dominated landscape, where the burrowing owls roosted and nested primarily in tunnels excavated by California ground squirrels (*Spermophilus beecheyi*). The site is on the campus of the University of California, Davis, where the presence of burrowing owls has been documented for at least the last 25 years (C. Barrows, L. Pompeli, and T. Schulz pers. comm.). The owls were somewhat habituated to humans, were relatively tolerant of ambient noise and human activity, and were readily observed with binoculars and a spotting scope. To minimize any disruption of naturally occurring owl behavior, I used a stationary vehicle as a blind and made behavioral observations from distances of between 50–200 m.

Color-marking and Behavioral Sampling. Population studies that focus on reproductive behavior require that individuals be unequivocally recognizable, so I color-banded as many owls as I could capture during the four breeding seasons of this study. I color-marked 112 burrowing owls, fitting every owl with a unique combination of four leg bands (two per leg). I recorded reproductive affiliations (mated pairs) and genealogies (putative parentage) of all burrowing owls, based on daily censusing and behavioral observations.

DNA Fingerprinting. I sampled blood from all burrowing owls captured in 1987–88. I used the minisatellite DNA probe pV47-2 (Longmire et al. 1990) to obtain DNA fingerprints from 67 of the Davis burrowing owls. I similarly analyzed DNA from 25 burrowing owls from other populations in California and Canada, including 2 captive families with known pedigree (see Johnson 1996). I compared these 'foreign' samples to those from the Davis population in order to calculate the genetic similarity of burrowing owls known to be unrelated. I excluded the 'foreign' samples from data sets used to characterize the wild Davis population.

Determination of Genetic Parentage. I combined several independent approaches in an attempt to determine the paternity and maternity of wild burrowing owls. I looked for concordance among four measurements, each of which has been used individually to ascertain genealogical relationships. These measurements included: (1) multilocus fingerprint similarity coefficients for offspring-parent pairs, (2) similarity coefficients for pairs of siblings, (3) presence of locus-specific offspring bands, and (4) attribution to parents of specific multilocus bands.

Similarity Coefficients. The similarity of DNA fingerprints can be used, within limits, as an index to the genetic relationship of two individuals and to average relatedness among members of a population (Lynch 1988, 1991). The most basic measure of similarity is the proportion of DNA fingerprint markers (bands) shared by any pair of individuals, and it is calculated from the equation $S = 2N_{XY}/(N_X + N_Y)$, where: N_{XY} is the number of DNA fragments common to the fingerprints of both individuals X and Y; N_X is the total number of fragments found in the profile of X; and N_Y is the total number of bands in Y. Coefficients of similarity (S-values) can theoretically range from 0–1.

To characterize the expected distributions of DNA fingerprint similarities for burrowing owls having different genetic relationships, I calculated S-values for pairs of individuals with known coefficients of relatedness (r). These comparisons were based on DNA fingerprints of owls from known pedigrees (see Johnson 1996). Their S-values should therefore approximate those for unrelated individuals in a randomly-breeding panmictic population. Two frequency distributions of similarity values were obtained for these samples, specifically, one for first-degree relatives ($r = 0.5$, $n = 18$ pairwise comparisons), including parents-offspring and siblings, and one for "non-relatives" ($r = 0$, $n = 27$), which was based on comparisons of all adults, non-siblings, and adults with offspring that were not their own. Similarity coefficients for pairs of close relatives ($r = 0.5$) averaged 0.6280. In contrast, the mean value of S-coefficients for presumed nonrelatives was 0.2812. I subsequently used these background similarity values to evaluate wild burrowing owl parentage and within-population relatedness.

RESULTS

Parentage of Offspring. I was able to propose putative parent-offspring relationships for 44 young owls, based on presence and behavior of adults at nests. Functional parents were confirmed as the actual parents of approximately 80% of the young owls. However, for nine other offspring (20.5%), one or both of the functional parents could not have been the true parent(s). The data also revealed at least two unambiguous extra-pair fertilizations, together accounting for at least two of 31 progeny (6.5%) that were produced and sampled in 1988. A third such case may have occurred in 1988. If three extra-pair fertilizations did occur, then approximately 10% (or more) of the 1988 cohort resulted from copulations extraneous to pair-bonds. During the two years of genetic study (1987 and 1988), two of the 20 breeding territories were occupied by three adult burrowing owls. In both of these trios, each of the adults was a parent of at least some of the offspring. Four other offspring were reared by pairs of adults, neither of which was their true parent. Instead, these progeny were produced by other mated pairs, including two nearest neighbors and two second-nearest neighbors. I suspect that exploratory movement by preindependent juveniles was the reason for genetic parentage being attributed to other mated pairs. In total, within one month of emerging, at least 20% of the young burrowing owls no longer associated with the nest at which they hatched, but with another nest.

Putative Versus Actual Reproductive Success. For many adults, the DNA fingerprints sampled during the two years of genetic study revealed differences between the number of young that were actually their offspring and the number inferred from behavioral observations. A difference in the number of actual and putative offspring occurred in 19 of 42 (45.2%) parent-brood combinations. There were more discrepancies in 1988 (68.4%) than in 1987 (26.1%). In both years, 12 of the 32 adults (37.5%) participated in rearing young that were not their own.

Population Similarity and Relatedness. DNA fingerprint similarity coefficients averaged 0.3358 for wild adult burrowing owls in the Davis population. This estimate was based on 48 separate within-gel comparisons of adults, exclusive of mates. The average coefficient of similarity for random adults in the Davis population was not only higher than that for known nonrelatives in the pedigreed captive families (0.2812; see Johnson 1996) but was also higher than the average fingerprint similarity calculated from presumably panmictic comparisons (0.2768).

I examined, in more detail, explanations for the relatively high mean similarity among owls in the Davis population. To estimate the incidence of mating by close relatives in the Davis population, I derived the mean similarity of DNA fingerprints from mated burrowing owls, 0.3309, based on 11 within-gel sample comparisons, and compared this value to the mean degree of similarity in the Davis population at large, 0.3358. Surprisingly, the DNA profiles of members of the mated pairs were slightly less similar to one another than were those of unmated adult burrowing owls in the population.

CONCLUSION

Although the identities of true parents of burrowing owl offspring often agreed with parent-offspring relationships indicated by behavioral observations, a substantial proportion (20%) of the field-based inferences were wrong due to extra-pair fertilizations, joint nesting, brood mixing and coalescence, and possibly intraspecific nest parasitism. These previously undocumented aspects of burrowing owl mating biology collectively resulted in alloparenting by at least 37% of the adult owls. In addition, owls in this population apparently bred nonassortatively with respect to the local pool of adults. Most of these behaviors can be expected to enhance within-population genetic heterogeneity and contribute to variation in individual reproductive success. However, the Davis burrowing owl population exhibited a higher mean coefficient of genetic similarity than did a collection of geographically separated owl populations, suggesting that some inbreeding is occurring in this wild owl population, probably as a result of small deme size due to population subdivision. Because inbreeding enhances selection between groups at the expense of opposing selection within groups, it can be expected to counter the effects of brood mixing and unequal reproductive contributions, and facilitate the evolution of burrowing owl social behavior.

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REPRODUCTIVE PERFORMANCE OF BURROWING OWLS (*SPEOTYTO CUNICULARIA*): EFFECTS OF SUPPLEMENTAL FOOD

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ABSTRACT.—The role of food in limiting the number of offspring fledged from nests (reproductive output) was experimentally investigated in a migratory population of burrowing owls (*Speotyto cunicularia*) in Saskatchewan, Canada. Dead laboratory mice were provided to 12 of 26 owl pairs during egg laying in 1992. Food-supplemented owls laid slightly larger clutches and produced eggs of higher volume, but did not show higher hatching success or produce more hatchlings than did unsupplemented birds. Pairs that were supplemented during the nestling stage only ($N = 8$) exhibited less cannibalism and fledged more young than did unsupplemented pairs ($N = 11$). These preliminary results suggested that, although food intake restricted the number of eggs that burrowing owls laid, the total number of young produced at a nest was constrained by food only during the nestling period. Food intake was thus more limiting during brood rearing than during egg laying.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *food limitation; food supplementation; clutch size; egg volume; cannibalism; nestling stage.*

Desempeño reproductivo del tecolotito enano (*Speotyto cunicularia*): efectos de alimentacion suplementaria

RESUMEN.—El papel del alimento como limitante de crias volantones de los nidos (rendimiento productivo) se investigo experimentalmente en una poblacion migratoria de tecolotito enano (*Speotyto cunicularia*) en Sakatchewan, Canada. Ratones de laboratorio muertos se dieron a 12 de 26 pares de tecolotes durante el periodo de la puesta de huevos en 1992. Los tecolotes con alimentacion suplementaria pusieron mas huevos y produjeron huevos de mayor volumen, pero no mostraron mayor exito de empollo o produjeron mas pollos que las aves sin alimentacion suplementaria. Parejas que se suplementaron durante el periodo de cria solo (N = 8) mostraron menos canibalism y tuvieron mas jovenes volantones que las parejas sin suplementacion (N = 11). Estos resultados preliminares sugieren que a pesar de que el consumo de alimentos restringio el numero de huevos puestos por los tecolotitos enanos, el numero de juveniles producidos por nido estaba restringido unicamente por alimento durante el periodo de cria. El alimento entonces fue mas limitante durante la cria de la nidada que durante la puesta de huevos.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) has been designated an Endangered species in Canada (Wedgwood 1978, Wellicome and Haug 1995) because of an alarming decline in its population (James and Fox 1987, Haug and Oliphant 1990, Haug et al. in press). The decrease in habitat quality and availability that has resulted from the steady increase in agricultural and urban development is believed to be the factor ultimately responsible for this decline (Zarn 1974, Wedgwood 1978, Haug and Oliphant 1990, Schmutz et al. 1991, Haug et al. in press); however, proximate factors have yet to be identified (Wedgwood 1978, Haug 1985, James and Fox 1987).

Proximate factors can cause population declines by reducing either recruitment (the number of first-time breeders) or survival, or both (Temple 1986). Unfortunately, studying survival rates of Canada's burrowing owls is difficult because they spend half of each year wintering in unknown areas at least as far south as Mexico (James 1992), and their degree of nest-site fidelity has not been

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well documented (Schmutz et al. 1989). Therefore, at present, the most feasible approach for addressing the population decline in Canada is to identify factors on the breeding grounds that affect recruitment.

Food limitation in birds is a common problem resulting from human-caused habitat alteration (Temple 1986). Previous authors have suggested that natural food supply may constrain reproduction in burrowing owls. Butts (1973) proposed that availability of vertebrate prey in the spring limited the reproductive output of owls in Oklahoma. Gleason (1978) showed that brood size increased with proximity to irrigated agricultural areas in Idaho, implicating prey availability as the causal factor. However, these studies provide only circumstantial evidence to support the hypothesis that food limits reproduction. In this study, I investigated the effects of food intake on reproductive output (one component of recruitment) by manipulating the amount of food available to breeding burrowing owls.

The two periods of the breeding season most commonly thought to represent energetic "bottlenecks" for birds are the egg-laying and brood-rearing stages (Martin 1987, Arnold 1992). Separate food supplementation experiments were conducted during each of these two periods.

METHODS

Burrowing owls were studied in the Grassland Ecoregion of Saskatchewan (Harris et al. 1983) from mid-April to mid-August, 1992, on a site situated south of the cities of Moose Jaw and Regina. The majority of the study area lies on the Regina Plain with the southernmost portion extending into the Missouri Coteau. Intensive cultivation in this region has left a heavily-fragmented landscape (James et al. 1990). Consequently, most owls nest in small, heavily-grazed pastures that are interspersed among a variety of habitat types, including cereal crops, summer fallow, hayland, and other grassland.

In May, one to two weeks after each pair had chosen a burrow and began lining its entrance with nesting material, a wooden artificial nest burrow (ANB) was installed within the natural burrow. This method of ANB introduction yielded a nest-use success rate of 94% (17 of 18 burrows; see also Olenick 1990). An additional 11 pairs prepared nests in wooden ANBs that had been in place prior to 1992, for a total of 29 occupied boxes. ANBs enabled me to count and measure eggs, establish laying and hatching dates, and monitor chick mortality. Pellets were collected near nests, roost burrows, and favorite perches at 3-d intervals throughout the breeding season.

Supplementation During Egg Laying. Because disturbance in the nest chamber during early laying is thought to increase the frequency of nest abandonment (Olenick 1990), I used evidence from aboveground observations to estimate clutch-initiation date. Laying was considered to commence when a female began spending most of her time inside the nest burrow.

Since food supplementation often leads to earlier laying (Arcese and Smith 1988) and earlier clutches are typically larger (Nilsson and Svensson 1993), it is important to experimentally separate laying date and clutch size (Nilsson 1991) if effects on clutch size are to be directly attributed to food intake. Hence, pairs were ranked by their estimated date of laying and then alternately assigned to supplemented and unsupplemented groups to remove effects of initiation date. Actual initiation dates were later determined by backdating from egg counts conducted prior to clutch completion (one egg is laid every 36 hr; Olenick 1990). Actual laying dates were, on average, 2.7 d after estimated laying dates (range: 6 d after to 3 d before). Nonetheless, the distributions of actual laying dates did not differ between experimental and control pairs (mean Julian date [SE]: 128.4 [0.9] vs. 130.5 [1.1], respectively; Kolmogorov-Smirnov two-sample test, $P = 0.34$, two-tailed).

Each of fourteen pairs was provided with dead white laboratory mice at 3-d intervals, beginning on the estimated day of clutch initiation (mean Julian date [SE]: 125.7 [1.0]). Supplementation continued through egg laying unless the nest attempt failed. Pairs were provided with food at a rate of approximately 65 g/nest/d, corresponding to more than twice the daily existence metabolism of an adult burrowing owl in captivity (mean = 26 g; Marti 1973). Fifteen control (unfed) pairs nesting in ANBs were visited every third day and disturbed for the same amount of time as were supplemented pairs.

The proportion of white fur in a randomly chosen subset of collected pellets (143 pellets from 21 visits) was estimated visually to give a rough measure of the proportion of supplemental food in the diets of supplemented owls. White fur from laboratory mice was easily distinguished from light-colored fur of other small mammals.

Clutch sizes were determined by counting eggs shortly after clutch completion. Egg dimensions were measured to the nearest 0.01 mm with dial calipers, and egg volumes were calculated using Hoyt's (1979) equation: $V = 0.000507*L*B^2$ (where V = volume, L = maximum length, and B = maximum breadth). Egg-size comparisons were based on mean egg volume per clutch.

Supplementation During Brood Rearing. Each of five unfed pairs from the above experiment were supplemented with food every third day for 40 d, beginning at the date of first hatch (mean Julian date [SE]: 160.4 [1.0]). Four additional pairs nesting in natural burrows (where hatch date and initial brood size could not be determined), were fed during this same time period (mean Julian date of first feeding [SE]: 160.7 [0.7]). Food was provided at a rate of 65 g/nest/d early in brood rearing and was increased to 75 g/nest/d late in the nestling stage. Four of the control pairs from the first experiment (see above) nesting in ANBs and ten previously undisturbed pairs nesting in natural burrows served as controls during the nestling period. Nest contents in ANBs were checked every third day during feeding or control visits. Both tarsi on each nestling were color-

Table 1. Clutch size, egg volume, hatching success, and number of hatchlings for burrowing owl pairs supplemented with food during egg laying and for control pairs. Fledging success and number of fledglings for owls supplemented during brood rearing and for control owls.

	Treatment						Difference[a]	
	Supplemented			Unsupplemented				
Parameter	$\bar{x} \pm$ SE	Median	N	$\bar{x} \pm$ SE	Median	N	U	P
Egg laying								
Clutch size	9.3 ± 0.2	9.5	12	8.9 ± 0.2	9.0	14	110.0	0.08
Egg volume (cm^3)	11.29 ± 0.22	11.19	12	10.89 ± 0.11	10.90	13	105.4	0.07
Hatching success (%)	90.2 ± 2.8	90.0	11	83.8 ± 5.6	90.0	11	65.0	0.38
No. hatchlings	8.4 ± 0.3	9.0	11	7.6 ± 0.6	8.0	11	73.0	0.20
Brood rearing								
Fledging success (%)	100.0 ± 0.0	100.0	5	81.0 ± 8.7	17.5	4	17.5	0.01
No. fledglings[b]	7.3 ± 0.4	7.5	8	6.2 ± 0.3	6.0	11	66.0	0.03

[a] One-tailed Mann-Whitney U-tests.
[b] Fledglings from both artificial and natural burrows.

marked using felt pens, allowing individual identification. When tarsus width reached its maximum, nestlings were fitted with aluminum bands. Natural burrows were observed for 30-min bouts on three or more occasions late in the nestling period to determine the number of nestlings fledged. A nestling was considered to have fledged if it was observed at a nest or satellite burrow 40 d or more after hatch. The age of young at natural burrows was estimated by comparing their morphologic measures or levels of feather development to known-age young from ANBs.

To ensure that fed and unfed groups had similar initial brood sizes, nests were ranked by clutch size and then alternately assigned to each treatment. As a result, the distribution of initial brood sizes (range: 6–10 hatchlings) did not differ between fed and unfed treatments (mean [SE]: 7.4 [0.6], $N = 5$, vs. 8.3 [0.9], $N = 4$, respectively; Kolmogorov-Smirnov two-sample test, $P = 0.98$, two-tailed). This method of assigning pairs could only be performed when clutch sizes were known, so pairs in natural burrows were assigned to each treatment at random.

In birds of prey, cannibalism often results from food stress (Bortolotti et al. 1991). In the present study, cannibalism was defined as the consumption of the flesh of a conspecific, regardless of how death occurred, following Bortolotti et al. (1991). A mortality was considered to be cannibalism if the remains of a nestling (i.e., feathers, bones, or an aluminum band) were observed in an ANB, or if, early in the nestling period, a chick disappeared between successive nest checks (3-d intervals; Bortolotti et al. 1991).

Statistical Analyses. All statistical tests were performed using SYSTAT for Windows (Wilkinson 1992). To lower the probability of committing a type-II error due to small sample sizes, a type-I error probability of 0.10 was *a priori* deemed as acceptable for significance testing (Krebs 1989). Egg volume, % of eggs hatched, number of hatchlings produced, % of nestlings surviving, and number of young fledged were compared between fed and unfed treatments using Mann-Whitney U-tests. Student's t-tests were not used because small sample sizes precluded accurate testing of normality and homogeneity of variances. One-tailed tests were used because effects in only one direction are meaningful to the hypotheses tested (Sokal and Rohlf 1981, Korpimäki 1989, Simons and Martin 1990). Incidence of cannibalism was compared between treatments using a G-test for independence with 1000 random iterations.

RESULTS

Egg Laying and Incubation. Of the 29 pairs that initiated laying, three failed prior to clutch completion and therefore could not be included in the experiment. Two of these (one fed and one unfed) abandoned their nests after laying five eggs each. Also, one male from a food-supplemented pair was killed by a Swainson's hawk (*Buteo swainsoni*). The other 26 owl pairs completed and incubated their clutches.

White fur from laboratory mice constituted an average of 27% of the volume of analyzed pellets from experimental nests during egg laying. No white fur was found in the pellets of unsupplemented owls.

Females given extra food produced an average of 0.4 more eggs than did controls, representing a 4.5% increase in clutch size (Table 1). In addition, the eggs of fed pairs were larger than those of control pairs, averaging 0.4 cm^3 (3.7%) greater in volume.

Four nesting attempts failed late in the incubation stage: two pairs abandoned (one had been fed during egg laying and one had not), one pair deserted because of human disturbance, and one clutch (unfed) was depredated.

There was no difference in hatching success between birds that had been fed during egg laying and those that had not (Table 1). The total number of hatchlings in nests that had received extra food did not differ from that in nests that had not received extra food. Thus, the larger clutches and eggs of supplemented pairs did not result in larger broods, and therefore food addition during egg laying did not ultimately increase reproductive output.

Brood Rearing. Of the 23 broods used in the nestling-supplementation experiment, four failed to fledge any nestlings. One of nine (11%) supplemented broods and three of 14 (21%) unsupplemented broods were lost to predators.

Analysis of a 121-pellet subset collected during 20 separate visits to experimental nests during brood rearing showed that white fur composed 24% of the volume of pellets.

Survival of owlets was monitored at nine ANBs throughout the nestling period. Incidence of cannibalism was higher for unsupplemented broods (3 of 4 ANBs) than for supplemented broods (0 of 5 ANBs; G-test for independence, $G_{ran} = 6.96$, $P = 0.03$), resulting in a lower proportion of young being fledged by unfed pairs than by fed pairs (Table 1). Feathers, bones, and bands of cannibalized nestlings were found in pellets of both siblings and parents, and beheaded nestlings were sometimes found in caches with other prey. In every case, the victim was the smallest of nestlings remaining in the brood (TIW unpubl. data).

Supplemented pairs fledged between six and nine young from ANBs and between six and eight young from natural burrows. Unsupplemented pairs fledged between five and eight young whether nesting in ANBs or natural burrows. When natural and artificial burrows were considered together, supplemented pairs fledged significantly more young than did controls (Table 1). Fed pairs produced an average of 1.1 (17.3%) more fledglings than did unfed pairs.

DISCUSSION

The reproductive output of burrowing owls appears to be limited by food intake. Food-supplemented pairs produced slightly larger eggs and clutches, had a lower incidence of cannibalism, and produced more fledglings than did unsupplemented pairs. Because food supplementation was conducted at different stages of the reproductive cycle (as suggested by Hochachka and Boag 1987), I was able to determine that food intake was more limiting during brood rearing than during egg laying. These experiments were replicated in 1993 with larger sample sizes. Results from 1993 appear to agree with those from 1992 experiments, but the data have not yet been fully analyzed.

Food intake at the nest may be limited for many reasons: (1) habitat quality limits prey abundance or prey availability, (2) foraging areas are far from nesting areas, so energy costs of transporting prey are high, (3) weather limits the number of hunting hours or modifies the behavior of prey, making them less available. The third factor is beyond the control of management, but the first two potential limitations can be alleviated through habitat improvement: habitats that support abundant, available prey in the vicinity of active owl nests could be recreated or enhanced. Prey monitoring during the season and observation of habitat use by foraging owls would determine which habitat types would be most profitable to improve.

It may be common for birds of prey to be reproductively limited by food (Martin 1987, Newton 1989). Experimental food addition has resulted in increased fecundity in a number of species of raptors: Eurasian sparrowhawk (*Accipiter nisus*) (Newton and Marquiss 1981), Eurasian kestrel (*Falco tinnunculus*) (Dijkstra et al. 1982), and Tengmalm's owl (*Aegolius funereus*) (Korpimäki 1989, Hornfeldt and Eklund 1990). The increase in clutch sizes of Eurasian sparrowhawks with supplemental feeding occurred in poor-quality habitat (Newton and Marquiss 1981). Intensive land-use practices (cultivation for cereal crops and heavy grazing of prairie for cattle production) may have reduced the quality of burrowing owl habitat on much of the Canadian prairies by reducing the availability of natural prey. This would explain the response of burrowing owls in southern Saskatchewan to extra food. Owls nesting in Alberta in an area with restricted cultivation (15% of land area) and moderate grazing pressure, show higher reproductive output and are declining more slowly (Schmutz et al. 1991) than are owls in Manitoba and Saskatchewan (Haug et al. 1995). Schmutz et al. (1991) attribute these differences in breeding success to differences in natural prey supply among the areas. Supplementation studies conducted also in areas of low-intensity agricultural land use could substantiate this assertion.

For species such as the burrowing owl that are declining in numbers precipitously, it is desirable to promptly stabilize populations by slowing or halting their decline until ultimate causes can be identified and, if possible, corrected (Temple 1986). Food supplementation is a short-term management technique that will immediately increase burrowing owl reproductive output where prey supply is limiting. Feeding can be restricted to the nestling period, when additional food appears to have the greatest benefits. Over the long term, it may be worthwhile to increase prey supply through habitat restoration in the vicinity of nests.

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REPRODUCTIVE ECOLOGY OF THE BURROWING OWLS, *SPEOTYTO CUNICULARIA FLORIDANA*, IN DADE AND BROWARD COUNTIES, FLORIDA

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ABSTRACT.—From 1988–90 a study of the reproductive ecology of the burrowing owl (*Speotyto cunicularia floridana*) was conducted to determine breeding chronology and success in Dade and Broward Counties. Reproductive data for each of the three years revealed a higher percent of successful territories (54%) for 1990 than for 1989 (40%) and 1988 (41%). Owls occupying previously established burrows had a higher success in fledging young (63%) than those using newly excavated burrows (19%). Flooding was the primary cause (63%) for nesting failures. Car collisions accounted for 50% of known mortalities.

KEY WORDS: *burrowing owl;* Speotyto cunicularia floridana; *reproduction; Florida.*

Ecologia reproductiva del tecolotito enano, *Speotyto cunicularia floridana* en los Condados Dade y Broward, Florida

RESUMEN.—De 1988 a 1990 un estudio de la ecologia reproductiva del tecolotito enano se realizo para determinar el exito de la chronologia reproductiva en los condados Dade y Broward. Datos reproductivos para cada uno de los 3 años (1988–1990) muestran una tasa de reproduccion mas alta (54%) en 1990 que en 1989 (40%) y 1988 (40%). Los tecolotes que ocupaban madrigueras previamente establecidas tuvieron exito reproductivo mas alto de pollos volantones (63%) que aquellos que usaron madrigueras recian excavadas (19%). Inundacion fue la causa principal de fracasos en anidicaion. Colisiones con autos fueron la causa de 50% de la mortalidad conocida.

[Traducción de Filepe Chavez-Ramirez]

Burrowing owls, (*Speotyto cunicularia*), are small crepuscular owls found throughout North America, the West Indies (Cory 1891, Howell 1932), portions of Central America (Land 1970) and the western coast of South America (Jaksić and Marti 1981). In continental North America there are two subspecies. The western burrowing owl, (*S.c. hypugaea*), resides in the dry grasslands, prairies and farmlands (Coulombe 1971) of western North America. The Florida burrowing owl, (*S.c. floridana*), lives primarily in naturally occurring high sandy ground of central, eastern, and western Florida (Rhoads 1892, Bent 1961), pastures (Ligon 1963), airports (Owre 1978), as well as vacant and residential lots (Wesemann 1986).

Burrowing owls in Florida are presently expanding from their former range (Neill 1954). The burrowing owl was first recorded in Florida by N.B. Moore in 1874 (Courser 1979). Historically, this owl reproduced primarily in the central portion of the peninsula (Sprunt 1954). Large expanses of native wooded areas have been cleared with the augmentation of development, dairy production and agriculture (Tebeau 1971). Land clearing and supplemental fill have provided more habitat for the burrowing owl in Florida (Betz 1932, Ligon 1963, Garrido and Montana 1975, and Courser 1979).

In southern Florida, Dade and Broward Counties, burrowing owls have established nesting territories in airports, pastures, sports fields, golf courses, university and college campuses, parking lots, roadway medians and in the yards of private residences. Remaining pastures in Broward County are under extreme demand from development. To survive, the dairy industry has had to increase cattle densities to augment productivity. The higher number of cattle has increased contacts with the owls resulting in a higher number of destroyed burrows.

The burrowing owls' ability to successfully adapt to altered habitats is limited. The degree of development within a given site may determine the future success of these small raptors. The Nongame

Wildlife Program of the Florida Game and Fresh Water Fish Commission (FGFWFC) and the Audubon Society of Southwest Florida are correlating the percent cover of development within their study sites and the burrowing owls' ability to successfully fledge young. In the first three years of their study, 1987–89, they observed a decline in fledgling production when the development exceeded 75% of an area. Even though these owls have the ability to tolerate human intrusion, the decline of suitable nesting habitats may be their limiting factor (Wesemann 1986, Millsap 1988).

The purpose of this project was to document the reproduction and general ecology of the burrowing owl at three different study sites in Dade and Broward Counties between December 1987 and September 1990.

STUDY AREA AND METHODS

Study Sites. Three sites were chosen for this project: the Miami International Airport (Dade County), a dairy farm (Imagination Farms) and private residences (southwestern Broward County). Approval from all owners was given prior to working on their property.

MIA is located in western Dade County, has three runways on 1293 ha, 70% of which is developed and paved. There is continuing pressure for runway and terminal expansion to accommodate the increased flow of air traffic. The burrowing owls' territories are in the sandy medians between the runways, taxiways and the inner perimeter road. Most territories are located adjacent to the inner perimeter road. The second study site is Imagination Farms, Inc. in the southwest corner of Broward County in the town of Davie. It is a dairy farm covering 240 ha. The third study site contains five separate areas located in several residential developments and estates in southwestern Broward County: the town of Davie, Rolling Oaks, Sunshine Ranches Estates, the Rock Creek Residences in Cooper City, and Ivanhoe Estates.

Locating Owls. Burrowing owls were located while driving a vehicle on roads, through pastures and along the airport's roadways. The birds were located by looking for their bobbing motion (Thomsen 1971) or by locating the highly exposed sandy mounds at the entrance of their burrows. Active burrows had evidence of excavated soil and a clear unobstructed entrance. Decorated entrances identified the nesting burrows of a territory. Inactive burrows were usually obstructed with grass or weeds, and most had spider webs. Once the territories were well established the owls became highly visible.

Owl Identification. The burrowing owls were individually identified with a numbered USFWS aluminum band on one leg and a plastic numbered color band (Gey Band and Tag Co.) on the opposite leg.

Capture Techniques. The owls were caught using a variety of methods. The most successful technique was the use of a noose carpet attached to a 180 g weight placed at the entrance and perimeter of the burrow (Kahn and Millsap 1978, Bloom 1987). Bal-chatri traps were used on several occasions (Berger and Mueller 1959, Beebe and Webster 1976) with infrequent success. The final method involved approaching the burrow from the blind side and capturing the owls by hand by reaching down the burrow. This method proved most successful in catching young owls at the airport and residences. The noose carpet was most effective when the owls excavated or continuously moved around at the entrance of the burrows. Once captured, the owls were immediately wrapped in a cloth to act as a hood. This handling technique prevented injuries from tongue-snapping, a stress induced response. If a cloth was not readily available, the mandibles were held closed with fingers. While wrapped in the cloth, the owls were promptly banded in the event of an early escape.

An owl census was conducted weekly at each territory in all of the study sites. The census involved recording the total number of owls observed, the number of adults present, the total number of young, the total number of fledged young, and the number of banded owls. Census was conducted during the owls' breeding period, January–August.

Breeding Chronology. Breeding chronology was determined by the number of owls observed during weekly visits to the study sites. No attempts were made to differentiate between the young and adult owls for the chronology data. The highest weekly count of owls in a given month was used to plot the graph. The seasonality data were plotted with pooled data for each of the study sites. Productivity was determined by observing young outside the burrow and counting the number that successfully fledged from a territory. A territory was considered successful if one or more young fledged from it (Steenhof 1987). Mean values in results are followed by ± two standard errors. In 1988, field inexperience may have accounted for an overestimate in the number of territories observed in the study sites. Several pairs had satellite burrows (Thomsen 1971, Wesemann 1986) at distances of over 30 m that may have been mistaken for additional territories. The territories observed in 1989 and 1990 were closely scrutinized to minimize this potential error.

Data were analyzed by using statistical methods described in Sokal and Rohlf (1981) and with AbStat (copyright, Anderson-Bell Co. 1984) and Ecological Analysis (Eckblad 1986) statistical software packages.

RESULTS

Chronology. Three years of data show a late spring peak in burrowing owl numbers in all of the study sites (Fig. 1). Owls appeared in January, and sightings rapidly increased until about the month of June. Numbers peaked in late May and early June. During the following months, the sightings decreased as adults shifted to a more crepuscular and nocturnal behavior and the young dispersed to new areas. The onset of summer and the rainy season probably play major roles in the shift in behavior and in fledgling dispersal due to the flooding of burrows.

Productivity. Reproductive data for each of the years (1988–90) reveals a higher success rate

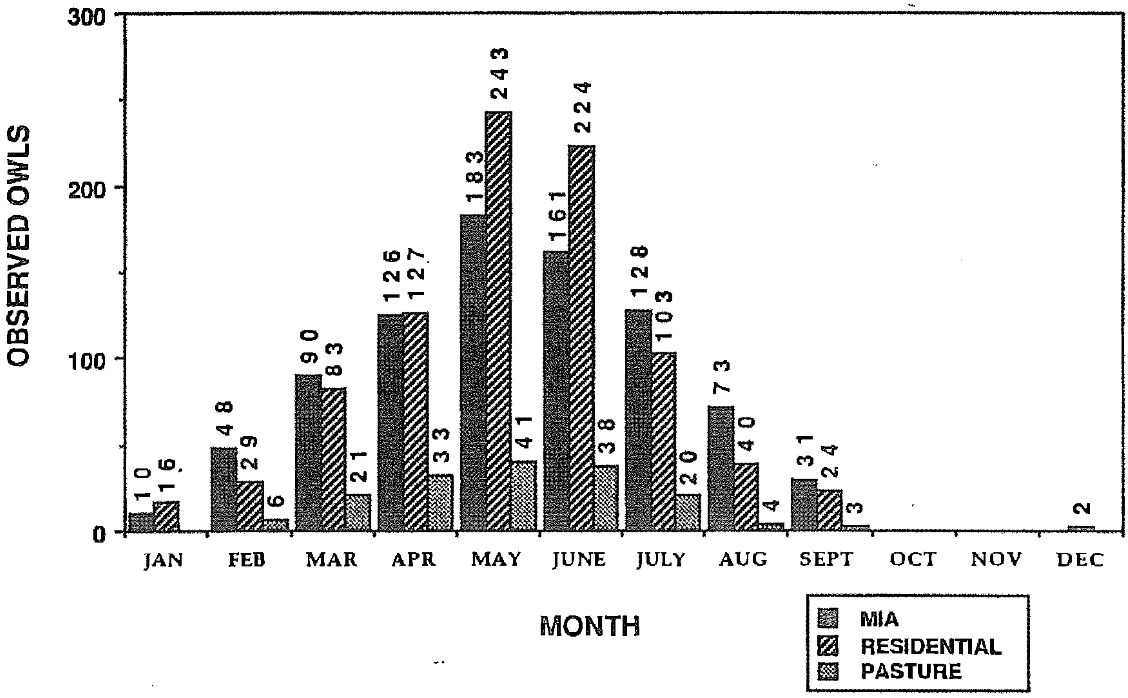

Figure 1. Number of burrowing owls observed by month during 1988–90.

(54%) for the 1990 season than the 1988 (41%) and 1989 (40%) seasons (Table 1). The pastures were the only study site that showed a relatively lower percent of successful territories in 1990 (14%, Table 2). This decrease is probably due to the increased cattle density and the infrequent mowing schedule that caused the vegetation to grow over the opening of the burrow. In 1990, the MIA and the residences both showed the highest percent in the number of successful territories (58%) and in the mean value of young fledging, at MIA $\bar{x}$ = 2.42 ± 0.5 and at the residences $\bar{x}$ = 2.84 ± 0.46 (Table 2).

The residential sites are an array of estates located in southwest Broward County. I added two additional study sites, Sunshine Ranches and Ivanhoe Estates in 1989–90, to the three study sites in 1988. From 1988–90 all residential study sites had an increase in the number of territories (Table 2). Except for Davie, all study sites also had an increase in the percent of successful territories.

Nest Decoration. Burrows were often decorated with a variety of materials found within or outside the boundaries of the territory. This included animal fecal material, aluminum foil, paper, string, other trash, and animal parts. Decorated burrows were a sign of occupied territories. Data suggested no relationship between decoration and nesting success. From 164 decorated territories, 84 (51%) fledged young and 80 (49%) failed. The use of

Table 1. Reproductive analysis for all territories from 1988–90 ±2 standard errors.

YEAR	NO. OF TERRITORIES	NO. OF SUCCESSFUL TERRITORIES	% OF SUCCESSFUL TERRITORIES	$\bar{x}$ YOUNG ALL TERRITORIES	$\bar{x}$ FLEDGED ALL TERRITORIES
1990	79	43	54%	2.80 ± .32	2.73 ± .34
1989	75	30	40%	2.46 ± .38	2.46 ± .38
1988	66	27	41%	2.56 ± .44	2.37 ± .40

Table 2. Burrowing owl reproductive data (±2 standard errors) from three study sites from 1988–90.

Study Site	No. of Territories	No. of Successful Territories	% of Successful Territories	$\bar{x}$ Young All Territories	$\bar{x}$ Fledged All Territories
1990					
Miami Int'l. Airport	24	14	58%	2.50 ± .5	2.42 ± .5
Residential	48	28	58%	2.90 ± .44	2.84 ± .46
Pastures	7	1	14%	4.00 ± 0	4.00 ± 0
1989					
Miami Int'l. Airport	27	12	44%	2.16 ± .54	2.16 ± .54
Residential	42	16	38%	2.75 ± .56	2.75 ± .56
Pastures	6	2	33%	2.00 ± 0	2.00 ± 0
1988					
Miami Int'l. Airport	32	15	47%	2.46 ± .52	2.33 ± .54
Residential	20	8	40%	3.00 ± .74	2.75 ± .72
Pastures	14	4	29%	1.75 ± .94	1.75 ± .94

dung has been shown to have little value in increasing a pair's potential to fledge young in these study sites of southeast Florida. From 193 territories in which dung was used, 87 (45%) fledged young and 106 (55%) failed.

Burrow Reuse. During the three years of this study 60% of the burrows were reused from previous years with a higher percentage in reproductive success rate than newly excavated burrows. From 84 territories with burrow reuse, 53 (63%) territories successfully fledged at least one young, while in 47 territories with new burrows, only 9 (19%) of them fledged young.

Nesting Failures. Of 123 known failures only 33 (27%) had clearly attributable causes. The primary reason for known nesting failures was flooding (N = 21, 63%). Other causes were collapse due to cow trampling (N = 6, 18%), human activities (N = 4, 12%), and predation (N = 2, 6%).

Mortality. Mortality data are for banded and unbanded specimens found in the study sites. Of 18 owls, 9 (50%) were killed by cars, 4 (22%) by drowning, 2 (11%) due to burrow collapse, 2 (11%) by predation, and 1 (5%) by electrocution.

Discussion

The Florida burrowing owl is currently listed as a species of special concern by the FGFWFC. The owls become more prevalent in January at the onset of the breeding season and the numbers peak in late May and early June. The increase in numbers has also been observed in New Mexico (Martin 1973), where numbers also peak in late May and early June. During the following months, sightings begin to decrease as adults shift to a more crepuscular and nocturnal behavior (Thomsen 1971), and most of the young begin to disperse to new areas (Martin 1973).

In areas categorized as heavy development (i.e., 75% developed) by Millsap (1988) the populations began to decline. In 1988, 60% of nesting failures in Cape Coral were a direct result of human activities (Millsap 1988). Courser (1976) documented a population decline due to development in a similar area near Tampa, Florida.

Comparing overall fledgling rate per breeding pair in studies of the western burrowing owl, the Florida burrowing owl has a lower productivity. Thomsen (1971) and Martin (1973) report fledgling rates between 2.2–5.5 per breeding pair for the western burrowing owl, while Millsap (1988) and Mealey (this report) report fledgling rates of 1.59–2.75 for the Florida burrowing owl.

In Dade and Broward Counties the population appears to be expanding to areas of new development. In areas that are zoned for residences with 0.40 ha or more, preliminary results indicate a stable population. This could be due to a limited number of people and fenced-in yards that provide protection. The residential areas of this study with 0.40 ha or more include Ivanhoe Estates, Sunshine Ranches, Davie, and Rolling Oaks. The mortality factors include flooding, human intolerance, and use of home pesticides.

Preliminary banding results (Millsap 1988) show territory fidelity. Currently, nesting behavior is used to identify the sexes. Incubation is believed to be primarily conducted by the females. Males provide food and select the territory. Usually, if a pair disappears from its territory it is assumed that the male is dead (B.A. Millsap per. comm.). Land alteration and development has contributed to the increases in Florida's burrowing owl population but eventually may be the cause of its decline.

Unlike the western subspecies, which need the protection of the natural habitat and the burrowing mammal population (Green 1983), the survival of the Florida subspecies may depend on the proper education of residents in documented key residential breeding grounds and by limiting the degree of alteration in future development sites (Millsap 1987). Burrowing owl breeding success at MIA of 58% (1990) coincides with success rates in Oregon of 57% (1980) and 50% (1981) (Green 1983) and at the Oakland Municipal Airport in California of 54% (1971) (Thomsen 1971). The continuing existence of the burrowing owl population at the MIA will be closely tied to the amount of development that takes place to accommodate future air travel.

Burrowing owls can only temporarily halt a project. The FGFWFC and the U.S. Fish and Wildlife Service issue permits to take or destroy inactive burrows outside of the nesting season. On occasion a permit may be issued during the nesting season to destroy a nest after the young have fledged. Care must be taken not to issue permits prematurely during the nesting season. Even though young may be defined as fledged they are still dependent on the primary and satellite burrows for a period of 30–60 days after they start flying.

Since land development is one of the primary causes for the owls' decline, improved and aggressive management strategies should be implemented to decrease known mortalities within successful breeding habitats. Simple requirements such as speed limit signs in conjunction with speed bumps would significantly decrease vehicle-related mortalities. Tax incentives should be awarded to contractors who voluntarily incorporate wildlife management and habitat restoration protocols into large development plans. Species coexistence and survival will depend on federal and state wildlife agencies to develop strict and enforceable guidelines/-policies on future development projects.

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LIFE HISTORY AND BEHAVIOR

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SELECTED MICROHABITAT VARIABLES NEAR NESTS OF BURROWING OWLS COMPARED TO UNOCCUPIED SITES IN ALBERTA

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ABSTRACT.—to examine the possibility that there may be more suitable nesting habitat in a grassland area of Alberta than burrowing owl (*Speotyto cunicularia*) pairs to fill it, I compared habitat parameters between nesting areas and systematically matched unoccupied grassland sites. There were no statistically significant differences in the density of grasshoppers, the number of American badger (*Taxidea taxus*) or ground squirrel (*Spermophilus* spp.) burrows, or the extent of cultivation. Although it is possible that one or more of the many factors not examined here limit owl numbers on the study area, it is also possible that factors operating on migration or in winter may limit survival of this threatened owl below carrying capacity.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *habitat; Canada; Alberta; prey; nesting; burrows.*

Variables de microhabitat seleccionadas cerca de nidos de tecolotito enano comparadas con sitios desocupados en Alberta.

RESUMEN.—Para examinar la posibilidad de que hay mas lugares adecuados para habitat de anidacion en areas pastizales de Alberta, que parejas de tecolotitos enanos para ocuparlos, compare parametros del habitat entre areas de anidacion con areas sistematicamente matched con sitios de pastizal desocupados. No se encontraron diferencias significantes en la densidad de chapulines, el numero de madrigueras de tejon (*Taxidea taxus*) y ardillon (*Spermophilus* spp.), o el grado de cultivacion. Aunque es posible que uno o mas de los factores no examinados aqui puedan limitar el numero de tecolotes en el area de estudio, tambien es posible que factores que operan en migracion o en areas invernales puedan limitar sobrevivencia de este tecolote amenazado que se encuentra bajo el limite de capacidad de carga.

[Traducción de Filepe Chavez-Ramirez]

Identifying the relative importance of factors that may influence the dynamics of "threatened" burrowing owl (*Speotyto cunicularia*) populations in Canada has proven difficult. The present study was sparked, among other observations, by reports from local landowners that burrowing owls have declined in recent decades in the absence of obvious changes in habitat or land use. This study was carried out in one of the least altered grasslands of Canada. Here, some native range remains, farmland long since abandoned has been revegetated (Dormaar and Smoliak 1985), and a ranching land use is regulated by the municipal government (Gorman 1988). Despite what superficially appears to be ample grassland suitable for burrowing owls, the density of owls recorded in a survey of 67 km^2 of land was 19.5 nests/100 km^2 (Schmutz 1993).

In this study I compared selected habitat and food variables around burrowing owl nests with systematically matched sites 1 km away. If no difference was discernible between nests and unoccupied sites, this might be consistent with the conclusion that more habitat is available than is presently occupied by the owls. I chose to measure grasshopper abundance because insects including grasshoppers are an important food source for owls in the population studied (Schmutz et al. 1991). A more important food source, mice and voles, was not included at this time because of the logistical difficulty of measuring the relative abundance of mice and voles in so many different localities. I studied the availability of burrows because all owls on the study area appear to nest in burrows (but see Cavanagh 1990). American badger (*Taxidea taxus*) burrows are sufficiently large to be used by the owls directly; ground squirrel (*Spermophilus* sp.) burrows need to be enlarged. I also recorded the extent of cultivation because it is thought to reduce habitat quality for the owls (Wedgewood 1976).

STUDY AREA AND METHODS

The study area was within a large expanse of rangeland used for grazing cattle. Approximately 15% of land was under cultivation for dry-land crop production. This region of mixed-grass prairie experiences low annual rainfall (27 cm) and for this reason sparse and short vegetation predominates. The gently undulating landscape supports a mixed *Stipa-Bouteloua-Agropyron* community with needle and thread grass (*Stipa comata*) and western wheatgrass (*Agropyron smithii*) prevailing (Smoliak et al. 1985). At one site of native grassland where burrowing owls nested regularly since at least 1986, the characteristic brown solonetzic soil had a 15-cm deep A-horizon of sand and a 13-cm deep B-horizon of clay. Especially in the clay layer, the generally dry soil is so well packed that it presumably presents significant barrier to excavation by burrowing owls.

I visited 34 nests at which at least one young was raised; 28 nests between 30 June–18 July in 1989 and six nests between 5–13 July in 1990. For comparison with occupied nests, I selected a "control" site 1 km north, except for seven nests which were in close proximity of one another, yielding 27 control sites. Although these control sites may be considered within an owl's 2.41 km^2 average home range (Haug and Oliphant 1990), home ranges can overlap greatly in this species. If the central point of a control site fell into a cultivated field, I selected a site to the east instead. Because of this choice the data from the control sites may underestimate the extent of cultivation in the region. However, this approach may make the comparisons from the point of view of what kind of habitat is available to burrowing owls more valid. Burrowing owls on the study area sometimes nested near a field, but to my knowledge not within it.

I recorded grasshopper numbers and amount of vegetation within a 30 × 30 cm wire frame (0.09 m$^{2)}$ tossed onto the ground at 10 m and 70 m from a nest or control site in each of the four cardinal directions. Many insects leapt as the wire frame touched the ground; those that remained were forced to move by stroking a hand over the ground. It proved impossible to identify the insects and count them at the same time. Therefore, I counted all insects that leapt from the ground within the wire frame. These potentially included grasshoppers (Acridoidea), leafhoppers (Cicadellidae) and froghoppers (Cercopidae). Vegetation was described as "barren" if the amount was judged <5 g/plot. When >5 g, live and dead stalks were cut at ground level and weighed on site.

Burrow openings, judged to be those of ground squirrels or badger (width >20 cm) according to size, were counted while driving a motorcycle along two 2 × 500 m line transects, extending north and south away from the burrow or the center of the control site. Within a 0.79-km^2 circle surrounding the nest or control site, I visually estimated the percentage of grassland, shrubland and cultivated land. This was done separately for each quarter circle and then summed.

I used contingency tables in the statistical analysis. I collapsed rows until no more than 20% of expected values were <5 (Conover 1971:152). I rejected the null hypothesis at $P < 0.05$.

RESULTS AND DISCUSSION

This study assumes that the habitat near burrowing owl nests is important to the owls not only for nesting, but also for feeding. While at least one member of an owl pair may range from 0.14–4.81 km^2 (Haug and Oliphant 1990) in search of food, Schmutz et al. (1991) have observed owls at at least 19 nests in the study area hunting insects from a vantage point near the nest.

Leaping insects and adult grasshoppers that flew ranged in length from approximately 2–15 mm. Although the majority of these insects were smaller than 4 mm, it is likely that most were actually grasshopper nymphs which could become large enough later to be used as food by the owls. Numbers of "grasshoppers" on plots varied from 0–15. Numbers were similar at 10 m (4.5/plot) and 70 m (4.9/plot) distances from nests. Using plots at 10 and 70 m distances combined, there was no significant difference between densities around nests compared with control sites (Table 1). These results suggest that grasshoppers were widely available throughout the study area. Therefore, it may be unlikely that grasshopper abundance, at least during the fledgling period, limited owl numbers.

Because avian and mammalian predators prey on burrowing owls, the availability of a suitable burrow for nesting or escape may be an important prerequisite (Coulombe 1971, MacCracken et al. 1985). Since it was impossible to judge the suitability of burrows for use by owls, I recorded all burrows when at least the entrance was open. I included ground squirrel burrows because the larger of these could conceivably be used by the owls. The abundance of ground squirrel burrows may also reflect badger activity and ground suitability for digging.

Burrows of ground squirrels and American badg-

Table 1. Density of grasshoppers, number of burrows and percent cultivation in the vicinity of 34 nests used by burrowing owls and 27 systematically selected sites in southeastern Alberta, 1989–90.

	Nest			Control Site					
Variable	Mean	SD	Range	Mean	SD	Range	χ^2	df	P
Grasshoppers	4.7	2.9	0–15	5.1	3.0	0–12	3.37	4	0.498
Burrows									
Squirrel	43.4	19.5	12–75	35.2	16.9	4–70	2.43	2	0.297
Badger	5.2	3.7	1–16	4.7	4.0	0–17	0.80	3	0.850
Grassland (%)	78.9	19.2	38–100	85.0	14.8	38–100			
Shrub cover (%)	4.8	3.7	0–13	6.2	4.2	0–15			
Cultivation (%)	16.3	19.0	0–60	8.8	15.6	0–62	2.23	2	0.328

er were abundant throughout the grasslands on the study area. A minimum of four ground squirrel burrows were present on all nest and control transects (Table 1). Only 4 of the 27 control transects had no badger burrow. While burrows of both badger and ground squirrels tended to be more numerous near nests in comparison to control sites, these differences were not statistically significant (Table 1). Thus, it is unlikely that burrow availability limited the breeding density of the owls.

Loss of habitat through land cultivation is thought to influence the distribution of burrowing owls (Wedgwood 1976). In contrast, Haug and Oliphant (1990) found that while fields with standing crops were avoided, so were overgrazed pastures. Fallow fields were used in proportion to availability. Cultivation on the study area resulted in large, widely scattered fields, either with crops growing or fallow. Patches of shrubs (primarily snowberry, *Symphoricarpos albus*) were generally small but frequent (present in 95% of nest and control areas combined). Of the nests sampled, 41% were located within 0.5 km of a field compared to 59% of control sites. Although slightly more area was under cultivation near nests (16.3%) compared to control sites (8.8%), there was no statistically significant difference among the percentage categories comparing nest and control sites (Table 1).

To measure a patch's potential ability to sustain the owls' cricetid or insect prey, I recorded the amount of above-ground vegetation present. I assumed that areas with above average amounts of vegetation would provide more escape cover and food for species in the owls' food chain (e.g., voles; Bock et al. 1984). Although fewer of the control sites (61.5%) compared to nest sites (76.5%; Table 2) were judged barren, this difference was not significant (x^2 = 5.26, df = 2, P = 0.072). These results suggest that systematically selected sites are at least as productive as occupied nesting areas.

The trend for lower vegetation density in the vicinity of nests compared to systematically selected sites may reflect the choices made by burrowing mammals more than burrowing owls. Although the land is largely flat, burrows tended to be more common on the higher and well-drained sites where moisture limitation is most severe. MacCracken et al. (1985) also interpreted differences between vegetation at burrowing owl nests and other sites in relation to burrowing mammals. In their study, the owls chose recently-vacated black-tailed

Table 2. The amount of vegetation in four subsamples each, at distances of 10 and 70 m from 34 burrowing owl nests and 27 control sites in southeastern Alberta, 1989–90.

	Nests				Control Sites			
Category	10 m	70 m	Total		10 m	70 m	Total	
"Barren"	30	22	52	76.5%	17	15	32	61.5%
6–17 g/plot	2	8	10	14.7%	5	5	10	19.2%
18–112 g/plot	2	4	6	8.8%	5	7	12	17.7%
Total	34	34	68		27	27	54	

prairie dog (*Cynomys ludovicianus*) burrows, whose mounds were in early stages of succession.

The habitat parameters studied provide only a narrow window into a variety of potential breeding requirements for burrowing owls. For instance, the parameters did not address the abundance of voles and mice, the influence of predators on site selection, or the change in food abundance throughout the season. This study suggests that if burrowing owl numbers in the region are low because of habitat, the factors causing this limitation are subtle. Future studies into the dynamics of burrowing owl populations should also take a view toward migration and wintering areas in the hope of discovering limiting factors.

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BURROWING OWL DEMOGRAPHY AND HABITAT USE AT TWO URBAN SITES IN SANTA CLARA COUNTY, CALIFORNIA

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ABSTRACT.—Data on several demographic and habitat choice parameters are reported for urban burrowing owls (*Speotyto cunicularia*) living at two sites in Santa Clara County: an "unintentional" preserve at Moffett Federal Airfield and a planned preserve at Shoreline Park. Differences in management practices and land use might be expected to result in significant differences between the owl populations at the two sites. Shoreline owls chose nest burrows in tallgrass fields more often than did Moffett Field birds, while the use of the other habitat types did not differ. The nest burrows themselves showed differences in several features. Owls at Moffett Field nested in burrows under cement or other hard surfaces significantly more often than birds at Shoreline. Shoreline owls were located on a hill or incline significantly more often than those at Moffett Field. Differences in management practices and availability of habitat features may help explain these findings. With respect to adult density, number of young fledged or pairs with emergent young, the very developed Moffett Field site was not found to have lower values than Shoreline Park. These findings indicate that the owls at both sites may be part of the same population. The data also show that urban sites can act as unintentional preserves and support owl populations if habitat features necessary for owls are provided.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *demography; habitat choice; urban preserves.*

Demografia y uso del habitat del tecolotito enano en dos sitios urbanos en el condado de Santa Clara, California.

RESUMEN.—Inforamacion sobre parametros demograficos y seleccion del habitat se reportan para el tecolotito enano (*Speotyto cunicularia*) que habitan dos sitios del condado de Santa Clara: una reserva "no intencional" en Moffet Federal Airfield y una reserva planeada en Shoreline Park. Se podria esperar que diferencias en practicas de manejo y uso del suelo resultara en diferencias significantes entre las poblaciones de tecolotes en los dos sitios. Los tecolotes de Shoreline usaron madrigueras en campos de pastizal alto con mas frecuencia que las aves de Moffet Field, mientras el uso de otros habitats diferio. Las madrigueras mostraron diferencias en varios aspectos. Los tecolotes de Moffet Field anidaron en madrigueras bajo cemento u otras superficies duras significativamente con mayor frecuencia que las aves de Shoreline. Los tecolotes en Shoreline se localizaban en cerros o laderas significativamente con mayor frecuencia que los de Moffet Field. Las diferencias en paracticas de manejo y disponibilidad de aspectos del habitat pueden explicar estos resultados. Con respecto a la densidad de adultos, numero de juveniles volantones, o parejas con juveniles emergentes el muy desarrollado Moffet Field no mostro valores mas bajos que Shoreline Park. Estos descubrimientos indican que los tecolotes de ambos sitios son parte de la misma poblacion. Los datos indican que los sitios urbanos pueden actuar come reservas no intencionales y soportar poblaciones de tecolotes si los aspectos del habitat necesarios para los tecolotes son provistos.

[Traducción de Filepe Chavez-Ramirez]

The western burrowing owl (*Speotyto cunicularia hypugaea*) is a small bird of prairie habitats which lives east of the Mississippi, north into Canada and south into Mexico. It is the only owl that routinely nests underground. The western subspecies does not dig its own burrows, but takes over burrows abandoned by colonial rodents such as prairie dogs (*Cynomys* spp.) and ground squirrels (*Spermophilus* spp.) (Zarn 1974), or solitary mammals such as badgers (*Taxidea taxus*) (Green 1983, Haug and Oliphant 1990).

Researchers and wildlife authorities have recognized that western burrowing owl populations are declining (Zarn 1974, Evans 1982, DeSante et al. 1992). Such declines seem to be particularly severe in California (James and Ethier 1989, DeSante et al. 1992), where the owl has Special Concern status.

Although human population growth and activity can affect their populations negatively, burrowing owls are quite tolerant of human presence and can adapt to human-altered landscapes (Wesemann and Rowe 1987; Trulio 1992). Burrowing owls are well-known inhabitants of airports, golf courses, school yards, and other short-grass habitats which provide burrows and a prey base (Thomsen 1971, Coulombe 1971, Trulio 1992). The fact that the Florida subspecies (*S. c. floridana*) has been increasing in some parts of urbanized Florida (Wesemann and Rowe 1987, James and Ethier 1989, Millsap pers. comm.), shows that healthy owl numbers and a large human population are not incompatible, at least up to a point (see Wesemann and Rowe 1987).

Despite their presence in urban habitats, it is not known whether western owl populations can persist in severely human-altered environments or what conditions may support their long-term survival. Studies of western burrowing owls in natural environments have provided data on demographics (Thomsen 1971, Coulombe 1971), habitat characteristics (see Zarn 1974 for review) and factors influencing burrow choice (Green 1983, Rich 1986). However, there has been little research on the factors leading to persistence or extinction of western burrowing owls in urban environments.

This paper presents data from a 3-year study of urban burrowing owls and compares two sites in Santa Clara County, California. The first, Moffett Federal Airfield, is an "unintentional" owl preserve with numerous military base activities including those related to the Navy airfield and NASA aircraft testing. The second site is Shoreline Park, a planned preserve and recreation area adjacent to Moffett Field, which supports activities such as golfing, hiking and biking. Much of the park is managed for wildlife use.

Given the different uses and management, the two sites might be expected to differ in demographic parameters and habitat choice by burrowing owls. As a park and wildlife preserve, Shoreline might be expected to provide higher quality habitat than Moffett Field and, therefore, support more owls per acre with a higher reproductive output. Owls at both sites should prefer undisturbed shortgrass fields and avoid tallgrass areas without perches. However, owls at Moffett Field might use tallgrass areas more often than Shoreline birds in order to escape human disturbances. Owls at Moffett Field might also choose burrows with features, such as a cement surface or a nearby fence, which could provide protection from surface disturbances. Possible differences between the two sites were tested with the following null hypotheses: Ho (1): Use of habitat types by nesting owls does not differ significantly between the two sites; Ho (2): Two features of nest burrows, location under a hard surface or on an elevation, do not differ significantly between the two sites; Ho (3): The reproductive output per pair at Shoreline is not significantly higher than Moffett Field; and Ho (4): The density of adult birds at Shoreline is not significantly higher than Moffett Field.

STUDY AREAS

Moffett Federal Airfield and Shoreline Park are located in Santa Clara County, 72 km south of San Francisco. Moffett Field is approximately 683 ha in size, of which approximately 250 ha are owl habitat. This base supports a large airfield with three aircraft hangers, NASA facilities, numerous administrative and residential buildings and is a Superfund site in the process of site identification and remediation. The primary human disturbances to owls include aircraft activity, grassland management practices such as discing, building and road construction, and daily human activity. Before 1 July 1994, approximately 8000 people worked at the base each day. California ground squirrels (*Spermophilus beecheyi*) are occasionally controlled in residential, administrative, and golf course areas using traps, but not regularly in areas that are without turf—a policy that has resulted in a large population of ground squirrels at the base.

Shoreline Park is a regional recreation and wildlife area established on a landfill which officially closed in 1983. The park is directly west of Moffett Field, and is separated from the base by an estuarine slough. Shoreline Park contains approximately 112 ha of potential owl habitat, including 38 ha of tall grassland and a 24 ha golf course. Much of the open grassland is managed for wildlife, particularly burrowing owls, by protecting undisturbed plant communities, prohibiting habitat destruction and restricting pedestrians. No poisons are used to kill squirrels and they are left undisturbed, except on the golf course where mechanical traps are used. Poisons are used occasionally to kill pocket gophers. The park receives up to a million visitors per year, or an average of 3000 people/day.

METHODS

Results cover the period from 1 January 1992–15 September 1994. Surveys of nearly all open lands at both sites were conducted on foot between

January and March of each year to locate occupied owl burrows. Burrows were recognized by the presence of owls or owl sign such as pellets and white droppings. All burrows and possible perching posts encountered were examined. Until approximately 15 September each year, at least half the known owl burrows were checked weekly for the number of adults and chicks. Two nesting burrows were observed each week for at least 2 h during the morning (700–1100 h) or evening (1600–2100 h) to get an accurate chick count and record behavior. Observations were made from cars or on foot using 10 × 50 binoculars. Burrow features recorded for this study included distance of burrows above grade and the presence of hard surfaces or fences. Chicks were considered fledged when they could fly strongly, which usually occurred 3–4 wk post-emergence.

Of the approximately 250 ha of owl habitat at Moffett Field, approximately 152 were included in the study. Approximately 112 ha of owl habitat at Shoreline were routinely surveyed.

Open, unpaved sites with burrows were considered potential owl habitat. Habitat was divided into four categories based on general vegetation management practices employed during the nesting period: short-grass (mowed or groundcover), tall-grass (unmowed), disced land, and barren (sprayed or graded).

At Moffett, tallgrass vegetation was never mowed or mowed only once during the nesting season and consisted primarily of Russian thistle (*Salsola kali*), star thistle (*Centaurea solstitialis*) and nonnative annual grasses which grew to a height of approximately 60–90 cm. The primary tall grass in the park, perennial rye grass (*Lolium perenne*), grew to a height of approximately 60 cm and was never mowed. In July 1992, NASA disced most of its open fields; i.e. plowed the top 10–15 cm of soil. Barren lands were levees, berms, road edges or fields which were often sprayed to remain vegetation-free. The total area of berms, road edges and bare earth could not be accurately determined at either site. Levees, a subset of barren lands, could be measured and this habitat type was used to indicate the extent to which owls nested in barren areas. Levees are embankments with water at the base during some period of the year.

Z-scores were used to determine whether habitats were used in accordance with their availability and whether burrow features at Shoreline differed significantly from those at Moffett Field ($P = 0.05$).

Table 1. Relative use of habitat types by adult owls at Shoreline Park and Moffett Field, 1992–94.

Habitat Type	% Total Area	% of Nest Burrows	Significance[a]
Shoreline			
Short grass	43%	29%	$z = -1.55$, NS
Tall grass	39%	32%	$z = -0.77$, NS
Levee[b]	11%	29%	$z = -3.00$, S
Disced	3%	7%	$z = -1.33$, NS
Moffett			
Short grass	28%	33%	$z = -1.00$, NS
Tall grass	65%	15%	$z = -8.33$, S
Levee[c]	4%	16%	$z = 5.00$, S
Disced[d]	18%	9%	$z = -0.88$, NS

[a] NS = not significant; S = significant.
[b] Amount of barren area could not be estimated, but contained 10 nest burrows. Levee habitat is used as an indicator of owl use of barren habitat.
[c] Amount of barren area could not be estimated, but contained 35 nest burrows. Levee habitat is used as an indicator of owl use of barren habitat.
[d] Disced lands occurred in 1992 only; percentages calculated for 1992 burrows and habitat.

T-tests were used to assess the difference between fledging success at the two sites.

Results

Table 1 provides the percentage of each potential owl habitat type at the two study sites and owl use of each habitat as measured by the presence of a nest burrow. Levee habitat was used as an indicator for owl use of barren sites. At Moffett Field, owls used levee habitats significantly more than expected based on their availability and significantly underused tallgrass sites. Mowed and disced sites were used in proportion to their availability. Shoreline owls used levee areas significantly more than expected and all other habitats in proportion with their availability.

Nest burrows at Moffett Field and Shoreline showed significant differences. At Shoreline, 68% of nests (21 of 31) were located on an incline or a mound, compared to 41% (28 of 69) Moffett Field nests, a significant difference ($z = 3.85$, $P = 0.05$). Nest burrows ($N = 9$) in hills or mounds in tallgrass habitat at Shoreline were an average of 1.4 m in elevation above the base of the hill. At Moffett Field, 45% or 31 of 69 burrows were located under a hard surface such as asphalt or behind a fence.

Table 2. Abundance and reproductive success of burrowing owls at Shoreline Park, 1992–94.

	1992	1993	1994[a]
Number of adults total[b]	23	20	13
Number of pairs total[b]	11	9	5
Pairs regularly observed	9	8	4
Pairs with emergent chicks	7	7	3
Percent of pairs with emergent chicks	78	88	75
Number of chicks fledged	21	15	14
Average number fledged/brood	3.0	2.5	4.7
Density of adults/ha	0.12	0.18	0.15

[a] Golf course excluded in 1994 from survey (24 ha).

[b] Only birds seen on more than one occasion were counted.

At Shoreline, only 19% of nest burrows (6 of 31) were similarly protected, significantly fewer than at Moffett Field ($z = 4.33$, $P = 0.05$).

Abundance and reproductive data for Shoreline and Moffett Field are given in Tables 2 and 3, respectively. Data from the two sites were comparable. Over the three years, Shoreline supported an average of 21 adults on approximately 112 ha, for an average density of 0.19 owls/ha. Of pairs observed, an average of 79% had emergent chicks. Over the three years, an average of 2.9 chicks were fledged/brood. Moffett Field supported an average of 43 adults on 152 ha for an average density of 0.28 adult owls/ha during the 3-year study period. The 3-year average for percent of pairs with emergent chicks was 75%, and the average number of chicks fledged was 2.5 chicks/brood. The average number of chicks fledged did not differ significantly between Shoreline and Moffett Field ($t = 0.975$, df = 15, $P = 0.05$).

DISCUSSION

Burrowing owls prefer open habitats or locations with perches which afford a good view of approaching predators (Zarn 1974, Green 1983). Green (1983) found that owls in Oregon avoided habitat with vegetation that impaired the owls' horizontal visibility and did not provide suitable perches. Habitat choice by owls at Moffett Field and Shoreline reflected these observed preferences, as owls at both sites used short grass habitat in proportion to its availability and nested on levee sites significantly more than expected. However, owls significantly underused tallgrass sites at Moffett Field, while Shoreline owls used tallgrass habitat in proportion with its availability. This difference resulted in the rejection of Ho (1), but not for the reasons expected. Owls at Moffett did not escape to tallgrass sites to avoid human impact, perhaps because they could not find burrows above the vegetation. Shoreline owls, on the other hand, were able to exploit tallgrass habitat by occupying burrows on mounds or an elevated site. Every burrow in tallgrass habitat at Shoreline was elevated above grade (10 of 10 burrows), while only 20% (2/10) of burrows in Moffett Field's tallgrass habitat were elevated.

Table 3. Abundance and reproductive success of burrowing owls at Moffett Field, 1992–94.

	1992	1993	1994
Number of adults total[a]	39	49	42
Number of pairs total[a]	19	23	19
Pairs regularly observed	15	19	19
Pairs with emergent chicks	11	14	15
Percent of pairs with emergent chicks	73	74	78
Number of chicks fledged	27	34	38[b]
Average number fledged/brood	2.5	2.4	2.9[b]
Density of adults/ha	0.26	0.32	0.26

[a] Only birds seen on more than one occasion were counted.

[b] Full counts of fledged chicks made on 13 pairs, which fledged 38 chicks total.

In general, the use of burrows on mounds or elevated sites differed between the two sites. Although mound availability could not be quantified at either site, it is likely that mounds and hills are less prevalent at Moffett Field than Shoreline. In the past, much of Moffett Field was leased as farmland and plowing fields would have flattened any mounds. As a closed landfill, Shoreline has never been farmed and when it was closed, the surface was purposely contoured to provide hills.

The use of tallgrass habitat at Shoreline and preferential use of levees at both sites suggest that the presence of mounds or elevation can increase the owl occupancy of a habitat. Levees are particularly attractive nest sites, since in addition to elevation, they are usually vegetation-free, well populated by ground squirrels and protected from flooding.

Disced lands were used in accordance with availability at both sites, but the small amount of area disced may not have allowed adequate statistical analysis.

Use of elevated burrows by Shoreline owls was one burrow feature which differed significantly between the two sites, resulting in the rejection of Ho (2). Another significant difference was the proportionately greater use of burrows under hard surfaces by Moffett Field birds versus Shoreline owls. It is likely that such burrows are more common at the very developed Moffett Field site, but this factor remains to be quantified. It is also possible that owls located under hard surfaces at the base may be more likely to survive disturbances than those not so protected. For example, discing fields can disturb or destroy owls nesting there (J. Buchanan pers. comm., J. Priest pers. comm.) and until 1993 many fields at the base were disced. Most of Shoreline has never been disced, sparing owls this pressure. Two fields outside the park included in the study are always disced and each year owls in those fields were located under a cement surface at the edge of the field. In natural habitats, owls use burrows under rocks (Rich 1984), lava flows (Gleason and Johnson 1985) and limestone (Coulombe 1971), perhaps as a protection against digging predators (Rich 1984).

Although habitat use and burrow features differed between the two sites, this study did not reveal differences in demographic parameters. Reproductive output values at the preserve were not significantly higher than at the more developed site. Although adult density at the two sites could not be statistically compared, Moffett Field actually had a denser population than Shoreline. Neither Ho (3) nor Ho (4) could be rejected, suggesting that both sites currently offer suitable habitat for owl survival and reproduction. This finding is very intriguing since the sites seem to differ so much in activity level.

While activities may differ, there are some important similarities. The general level of human and auto traffic at Moffett Field seems similar to Shoreline. In potential owl habitat, Moffett has approximately 0.07 km of roads/ha, compared to 0.06 km of roads and paved pathway/ha at Shoreline. An average of 3000 people visit Shoreline daily (16.5 people/ha) compared to the approximately 8000 people employed people at Moffett (21.9 people/ha) (Dept. of Navy, 1990). People and active land uses at both sites are restricted to specific areas, while the large, open areas where owls tend to live are generally less disturbed.

Other aspects of land management at Moffett Field help provide habitat of similar quality to Shoreline. Large areas of tallgrass provide foraging habitat; other areas are constantly kept short and provide nesting habitat; and ground squirrels are abundant on the open fields and golf courses.

The similar demographic results may also indicate that Shoreline and Moffett owls are part of the same population. The two sites are immediately adjacent to each other with no barriers to owl movement between them and owls may be sharing the positive and negative features of both areas. On a larger scale, the abundance and reproductive success of owls at the two sites may be reflecting conditions of the greater Santa Clara Valley region.

This study suggests that owls can survive on very urbanized sites, which can function as unintentional reserves, if those sites are managed to provide features required by owls. Such features include large open fields for foraging and short-grass sites for nesting. These data suggest that habitat can be enhanced for owls by installing dirt mounds and allowing ground squirrels to dig burrows. Artificial burrows in mounds can be used to provide immediate nest sites for owls (Henny and Blus 1981, Trulio 1992). Burrows under hard surfaces may attract nesting birds and protect them from inadvertent disturbances. Mowing around nest burrows and restricting constant foot or auto traffic help keep sites attractive to nesting owls. Avoiding biocide use is important for ensuring healthy populations of other species upon which owls depend.

Ultimately, integrating burrowing owl habitat into urban environments may prove to be an important method for protecting this species.

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BURROWING OWL SEXUAL AND TEMPORAL BEHAVIOR DIFFERENCES (ABSTRACT ONLY)[1]

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ABSTRACT.—In the field season of 1992, a night-vision scope was used to collect burrowing owl (*Speotyto cunicularia*) behavioral data during darkness comparable to that collected in daylight. Diurnal and crepuscular/nocturnal behaviors, particularly foraging behaviors, were split into prehatch and posthatch seasons and analyzed separately. During the prehatch period, preliminary investigations showed that prehatch comfort movements (e.g., preening, stretching) ($P = 0.0054$), resting ($P = 0.0097$), and alert ($P = 0.0059$) behaviors were greater diurnally, while out-of-sight ($P = 0.0021$) and feeding ($P = 0.0035$) were greater during crepuscular/nocturnal hours. During the posthatch period burrowing owls locomoted more nocturnally ($P = 0.0002$) and performed comfort movements more frequently diurnally ($P = 0.0042$). When the sexes were analyzed separately, females rested ($P = 0.0127$) more during daylight in the posthatch period. Foraging bouts when an owl returned with a small mammal ($\bar{x} = 327$ seconds) were longer ($P = 0.0001$) than those resulting in an insect capture ($\bar{x} = 205$ seconds). Male foraging bouts ($\bar{x} = 257$ seconds) were also longer ($P = 0.0001$) than female ($\bar{x} = 193$ seconds). Males took more small mammals proportionally (15%) than did females (2%) ($P < 0.05$). Results indicate increased burrowing owl foraging activity of both small mammals and insects at dusk and into nightfall.

KEY WORDS: *burrowing owl*; Speotyto cunicularia; *behavior*; *foraging*.

Diferencias de conducta por sexo y temporales de Tecolotito Enano

RESUMEN.—Un telescopio de vision nocturna se utilizo para colectar informacion de la conducta del tecolotitio enano (*Speotyto cunicularia*) durante periodos de obscuridad para comparar con datos collectados durante el dia. Conducta diurna y crepuscular/nocturna, particularmente conducta de forageo, se dividieron en temporadas antes y despues del empollo y se analizaron por separado. Durante el periodo antes de la salida del huevo, investigaciones preliminares mostraron que moviminetos de comodidad (estirar, arreglo de plumas) ($P = 0.0054$, descanso ($P = 0.0097$) y alerta ($P = 0.0059$) eran conductas mas comunes durante el dia, mientras que las categorias fuera de vista ($P = 0.0021$) y comer fueron mayores durante horas crepusculares/nocturnas. Durante el periodo despues de la salida del huevo los tecolotitos mostraron mas locomocion durante la noche ($P = 0.0002$) y realizaron movimientos de comodidad con mas frecuencia durante el dia ($P = 0.0042$). Cuando los sexos se analizaron por separado, las hembras descansaron ($P = 0.0127$) mas durante el dia durante el periodo despues de la salida del huevo. Tiempos de forageo cuando el tecolote retorno con un pequeño mamifero ($\bar{x} = 327$ segundos) fuerom mas largos ($P = 0.0001$) que aqeullos que resultaron en la captura de un insecto ($\bar{x} = 205$ segundos). Los machos capturaron mas pequeños mamiferos proporcionalmente (15%) que las hembras (2%) ($P < 0.05$). Los resultados indican que la actividad de forageo del tecolotito enano de insectos y mamiferos aumenta durante la puesta del sol y en la noche.

[Traducción de Filepe Chavez-Ramirez]

[1] For further details see Pezzolesi, L.S.W. 1994. The western burrowing owl: increasing prairie dog abundance, foraging theory, and nest site fidelity. Master's thesis. Texas Tech. Univ., Lubbock, TX.

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TERRITORY FIDELITY, MATE FIDELITY, AND DISPERSAL IN AN URBAN-NESTING POPULATION OF FLORIDA BURROWING OWLS

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ABSTRACT.—From 1987–91 we studied an urban population of Florida burrowing owls (*Speotyto cunicularia floridana*) on a 35.9-km^2 study area in Cape Coral, Lee County, Florida. During this period our study population increased from 149 occupied territories in 1987 to 246 in 1990; a total of 785 nesting attempts was monitored. From 1987–90, 601 owls, about 25% of breeding adults and 20% of nestlings in each year, were banded. Nearly all banded breeding adults were identified in subsequent years, and 245 individuals were reencountered at least once. Reencounter rates averaged over the years 1988–91 were 68% for adult males, 59% for adult females, and 19% for owls banded as nestlings. Natal dispersal distances differed significantly between sexes. The median natal dispersal distance was 414 m for males and 1116 m for females. About 36% of males settled on their natal territories, and at least 11% mated with their mothers; only one female (3%) settled on her natal territory. Adults had a high degree of fidelity to breeding territories, with 83% of males and 74% of females breeding on the same territories for at least two consecutive years. Territory fidelity appeared to increase with age in both sexes. There were no clear patterns that preceded territory shifts, except that females usually moved to a new territory after the death of a mate, whereas males generally stayed on the same territory regardless of the status of their prior mate. When breeding dispersal did occur, females moved further than males; median breeding dispersal distance was 230 m for females and 96 m for males. Among pairs where both adults survived between years, 92% remained together. Patterns of dispersal and territory and mate fidelity in our study population suggest male experience on a given territory may be an important factor in determining reproductive success.

KEY WORDS: *burrowing owl*; Speotyto cunicularia floridana; *fidelity*; *nesting*; *Florida*; *dispersal*; *urban*.

Fidelidad territorial, fidelidad de pareja, y dispersion en una poblacion de tecolotitos enanos de Florida en un area urbana

RESUMEN.—De 1987 a 1991 estudiamos una poblacion urbana de tecolotito enano (*Speotyto cunicularia floridana*) en una area de estudio que comprendia 35.9-km^2 en Cape Coral condado de Lee, Florida. Durante este periodo nuestra poblacion de estudio aumento de 149 territorios ocupados en 1987 a 246 en 1990; un total de 785 atentos de anidacion se monitorearon. De 1987 a 1990, 601 tecolotes, aproximadamente 25% de los adultos reproductores y 20% de los pollos en cada año se anillaron. Casi todos los adultos anillados fueron identificados en años subsequentes y 245 individuos se encontraron cuando menos una vez. La tasa promedio de reencuentro para los años 1988–91 fueron de 68% para machos adultos, 59% para hembras adultas, y 19% para tecolotes anillados en el nido. Distancias de dispersion natal diferieron significativamente entre los sexos. La distancia media de dispersion natal fue de 414 m para machos y 1116 m para hembras. 36% de los machos se establecieron en sus territorios natales y al menos 11% aparearon con sus madres; solo una hembra (3%) se establecio en su territorio natal. Adultos tuvieron alta fidelidad a sus territorios de reproduccion con 83% de machos y 74% de las hembras reproduciendose en el mismo territorio cuendo menos 2 años consecutivos. Fidelidad a territorios parece ser mayor con edad en ambos sexos. No hubo patrones claros que anticipara cambios en territorios, excepto que hembras usualmente se cambiaron a un nuevo territorio despues de la muerte de su pareja mientras los machos generalmente permanecian en el mismo territorio, sin importar la condicion de su previa pareja. Cuando dipsersion reproductiva ocurrio, las hembras se desplazaron mas lejos que los machos. De las parejas en las que ambos adultos sobrevivieron entre años 92% se mantuvieron juntas. Patrones de dispersion y fidelidad territorial y de pareja en nuestra poblacion sugiere que la experiencia del macho en determinado territorio es un importante factor que determina exito reproductivo.

[Traducción de Filepe Chavez-Ramirez]

Despite its wide range and history of scientific interest, many aspects of the biology of the burrowing owl (*Speotyto cunicularia*) remain poorly understood. This is particularly true for nonmigratory subtropical and tropical populations of this widespread species. Although the burrowing owl is garnering conservation attention throughout much of its North American range, it is significant that at least two Caribbean island populations of this species have gone extinct in recent times (AOU 1957).

The Florida burrowing owl (*S. c. floridana*) is an extant subtropical population that is of some concern. This race of burrowing owl occurs throughout peninsular Florida and the Bahama Islands. Unlike most western burrowing owl populations, Florida burrowing owls usually excavate their own nest burrows, although they will use burrows of gopher tortoises (*Gopherus polyphemus*) and nine-banded armadillos (*Dasypus novemcinctus*) when available (Haug et al. 1993). As with many other arid-adapted taxa in Florida, burrowing owls probably colonized the state from western North America during early- to mid-Pleistocene glacial periods when a circum-Gulf arid dispersal corridor existed (Webb 1990). Florida burrowing owl populations have probably been isolated since the close of the Wisconsinan stage of the Pleistocene, which was at its height 20 000 years before the present (Webb 1990). Early records of burrowing owls in Florida were mainly from the central peninsula (Ridgway 1914, Bent 1938). Burrowing owls began a range expansion in Florida in the 1940s that continues to the present, presumably facilitated by land-clearing operations along the coasts and in the northern peninsula and panhandle. In the early 1940s burrowing owls were found breeding in Hernando County in west-central Florida (MacKenzie 1944), by 1954 nesting was documented in Marion County in northcentral Florida (Neill 1954), and in 1992 a breeding population was discovered in the Florida panhandle in Okaloosa County (B. Millsap unpubl. data).

Despite its expanding range, the Florida Game and Fresh Water Fish Commission lists the Florida burrowing owl as a Species of Special Concern (Wood 1992), and the agency has initiated several conservation projects for this subspecies. One of the greatest perceived threats to this race is habitat development and resultant land use changes. Ironically, the very land use changes that create suitable new habitat for burrowing owls in Florida also destroy it, and there are many cases where thriving local populations have become extirpated over the span of a few years (Courser 1976). To better understand the causes of burrowing owl population changes in developing areas, the Game and Fresh Water Fish Commission and Audubon Society of Southwest Florida initiated a study of burrowing owls in an urbanizing area of southwest Florida in 1987. Wesemann and Rowe (1986) conducted preliminary work on this study population in 1985 and 1986; we continued and expanded their work to include banding and monitoring adults and young and determining reproductive success. This paper presents information collected on dispersal and mate and territory fidelity in this study population.

STUDY AREA AND METHODS

Observations were made between 1 January 1987 and 10 July 1991 on a 35.9-km^2 study area in Cape Coral, Lee County, Florida (Fig. 1). The study area consisted mainly of single-family homes interspersed with vacant lots. Vacant lots, where most nest burrows were situated, were maintained as disclimax grasslands by regular mowing. Climate in Cape Coral is subtropical, with an annual mean temperature of 23.1°C. Temperatures below 0°C are rare; lowest daily mean temperature for January (the coldest month) is 10.9°C. Precipitation averages 125.7 cm annually, and 75% of rainfall occurs between May–September (climate data from NOAA climatological data summaries for Fort Myers, Florida, 20 km southeast of the study area).

From January–March, 1987–91, we drove all roads in the study area searching for burrowing owl nest burrows. This approach is known to locate all but a small percentage of nests (Wesemann and Rowe 1987). Burrows attended by two adult owls or decorated with shredded paper and grass were considered occupied territories. Data on the number of occupied territories on our study area in 1986 were collected using methods described by Wesemann and Rowe (1987). From 1987–90, adult and juvenile burrowing owls were captured with noose carpets placed at the burrow entrance and banded with U.S. Fish and Wildlife Service bands and colored leg bands. Nearly all adults attending nests on the study area were checked for bands annually from 1988-91. Additionally, from 1988–90, we searched for banded burrowing owls at territories in a 3.2-km-wide band immediately north of our study area, as well as south of our study area to the

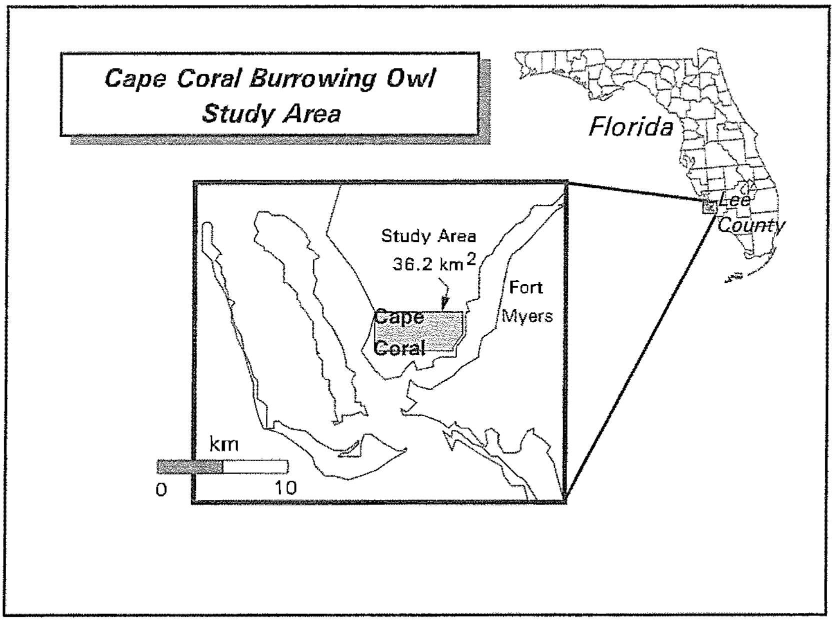

Figure 1. Study area in Cape Coral, Lee County, Florida.

southern terminus of the Cape Coral peninsula. When banded owls were resighted on the study area or elsewhere, we confirmed identification by reading band numbers with spotting scopes or binoculars or by retrapping. The sex of breeding adults could usually be determined at a distance by plumage (males were paler than females due to increased sun-bleaching (Thomsen 1971, Butts 1973, Martin 1973)) or behavior (Thomsen 1971). Breeding females with eggs or small young could be distinguished in the hand by the presence of a large, vascularized incubation patch. We were unable to determine the sex of nestlings when they were initially banded, but most that were subsequently reencountered as breeders were sexed. Nests on the study area were visited weekly in the early morning or late afternoon (when owls were active aboveground) throughout the nesting period (mid-February through early July) to determine fledging success and estimate brood size at fledging.

We analyzed data using statistical procedures in SYSTAT (Wilkinson 1990). Parametric procedures were used when raw variates or transformed variates appeared normally distributed. In cases where normality was suspect, we used nonparametric tests. In these cases we report medians as our measure of central tendency and interquartile ranges (i.e., the interval around the median that contains 50% of all observations) as our measure of data dispersion.

We define *natal dispersal* as dispersal by a burrowing owl from the territory where it hatched to the territory where it first bred. *Breeding dispersal* refers to dispersal from a previous breeding territory to a new territory or to a new burrow on the same territory if the prior year's nest burrow was occupied by another pair of breeding adults. The term *reencounter* refers to the identification of an owl banded in a previous year; in numerical tallies, individuals identified in multiple years accounted for multiple reencounters, but no owl accounted for more than one reencounter in any one year. In reporting ages of burrowing owls, we use the following terms: *second year* (SY) for owls in their second calendar year of life; *third year* (TY) for owls in their third calendar year of life; *fourth year* (FY) for owls in their fourth calendar year of life; *after hatching year* (AHY) for owls of uncertain age but at least SY or older; *after second year* (ASY) for owls of uncertain age but at least TY or older; *after third year* (ATY) for owls of uncertain age but at least fourth year (FY) or older; and *after fourth year* (AFY) for owls of uncertain age but in at least their fifth calendar year of life.

RESULTS

Population Size. From 1987–90 we located and monitored 785 occupied burrowing owl territories on our study area. The number of occupied territories increased annually, from 149 in 1987, to 175 in 1988, 213 in 1989, and 248 in 1990. Wesemann and Rowe (1987) reported 133 occupied territories on our study area in 1986. Because our survey efforts and approach remained relatively constant among years, we attribute the increase in the number of occupied territories to an increase in population size over the study period.

Reencounter Rates for Banded Owls. From 1987–90, we banded 601 burrowing owls on our study area: 307 nestlings of unknown sex, 116 adult

Table 1. Reencounter rates for banded Florida burrowing owls, Cape Coral, Florida, 1988–91.

	% OWLS ALIVE PRIOR YEAR THAT WERE REENCOUNTERED				
AGE[a]	1988	1989	1990	1991	MEAN (SD)[b]
SY	31	20	17	10	19 (1.2)
>ASY male	79	68	62	64	68 (0.7)
>ASY female	69	61	54	51	59 (0.7)

[a] Age codes are as follows: SY (second year) = burrowing owls banded as unsexed nestlings the prior year; >ASY (after second year) male and >ASY female = burrowing owls of known sex that were SY or AHY the prior year when first banded or when reencountered.

[b] Means were calculated from arcsine-transformed proportions for each year, such that $N = 4$ in each case. Arcsine-transformed mean proportions differed significantly among age/sex categories (one-way ANOVA, $F = 40.4$, df = 2/9, $P < 0.0001$). A Bonferroni post-hoc test indicated that mean reencounter rates for >ASY males and females were not significantly different ($P > 0.05$), but that both differed significantly from the mean reencounter rate for SY owls ($P < 0.0001$).

males, 153 adult females, and 25 adults of unknown sex. Overall, about 25% of breeding adults and 20% of young on our study area were banded each year. From 1988–91 we reencountered 245 (41%) of these owls at least once, 131 (27%) were reencountered in two or more years, 52 (17%) in three or more years, and 11 (8%) in four years. An average of 68% of adult males, 59% of adult females, and 19% of nestlings were known to survive between years (Table 1). Mean reencounter rates differed significantly between established adults and second-year owls, but not between sexes of adults (Table 1).

Natal Dispersal. From 1988–91 we reencountered, as breeders, 31 female and 28 male burrowing owls that had been banded as nestlings. Median natal dispersal distance of females was 1116 m (interquartile range = 440–1725 m); median natal dispersal distance for males was 414 m (interquartile range = 150–850 m) (Fig. 2). Natal dispersal distances differed significantly between sexes (Mann-Whitney $U = 484.0$, df = 1, $P = 0.001$).

The mean distance between nearest adjacent occupied nest burrows on our study area in all years was 176 m (SD = 135.8, $n = 785$). Of the banded nestlings reencountered as breeders, one female

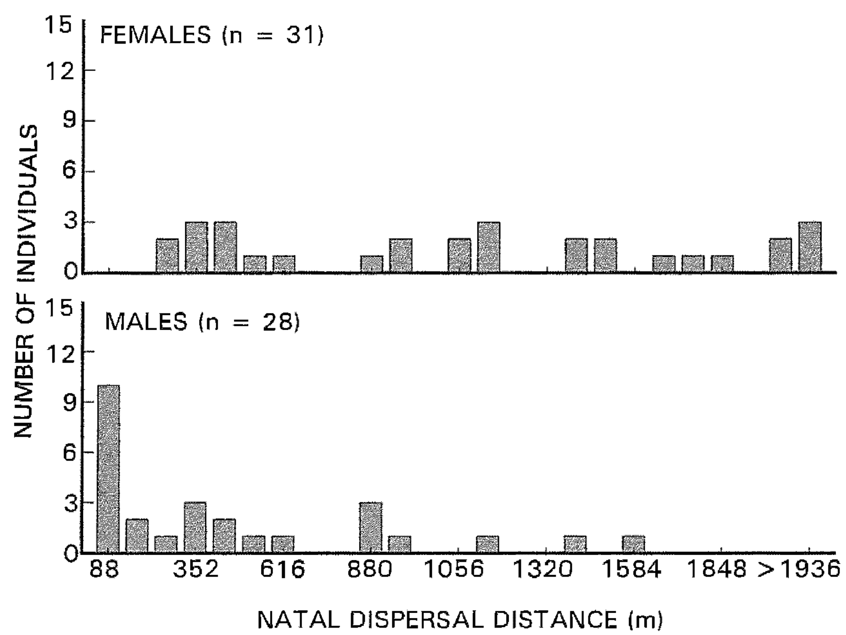

Figure 2. Histogram of natal dispersal distances of burrowing owls from Cape Coral, Lee County, Florida, 1988–91. We defined natal dispersal as dispersal by a burrowing owl from the territory where it hatched to the territory where it first bred.

Table 2. Fidelity to prior year's territory by Florida burrowing owls known to have survived between years, Cape Coral, Florida, 1988–91.

	% of Reencountered Birds Found on Same Territory	
Age[a]	Male	Female
SY	36 (10/28)	3 (1/31)
ASY/TY	78 (77/98)	68 (69/101)
ATY/FY	91 (42/46)	73 (41/51)
AFY	83 (20/24)	83 (15/18)

[a]Age codes are as follows: SY = second year (individuals in their second calendar year); ASY = after second year (individuals in at least their third calendar year); TY = third year (individuals in their third calendar year); ATY = after third year (individuals in at least their fourth calendar year); FY = fourth year (individuals in their fourth calendar year); AFY = after fourth year (individuals in at least their fifth calendar year).

(3%) and 10 males (36%) nested in their natal burrow or within one-half the mean inter-nest distance (i.e., within 88 m) of their natal burrow. Three of these males (11%) paired with their mother on their natal territory; in only one case was the father banded, and in this instance he was found paired with a new female at a new burrow 20 m away.

Territory Fidelity. From 1988–91, we recorded 399 reencounters of Florida burrowing owls of known sex. Pooled across sex and age classes, 273 (68%) reencountered individuals remained on the same territory between years (Table 2). However, rates of territory fidelity were not independent of age or sex. Among second-year owls, more males than females remained on their natal territory than expected by chance (G = 7.56, df = 1, P = 0.006). For older age classes, territory fidelity was independent of sex (G = 0–2.69, df = 1 for all comparisons, $P > 0.10$ for all comparisons). Age appeared to influence territory fidelity among both sexes. Tested separately, and as would be expected, both male and female SY owls were less prone to remain on their natal territory than older adults were to remain on their prior-year's breeding territory (for males G = 27.9, df = 1, P = 0; for females G = 58.3, df = 1, P = 0). Among adults older than SY, fidelity was not independent of age (G = 6.68, df = 2, P = 0.035). Comparison of simultaneous confidence intervals for proportions using the Bonferroni approach (Byers and Steinhorst 1984) indicated that moves by ASY and TY adults occurred more often than expected relative to moves by adults older than three years of age (sexes were pooled for this analysis because territory fidelity was independent of sex for ASY and older adults).

From 1988–91, 53 reencountered adult males and 57 reencountered adult females vacated a territory, switched burrows on a territory, or moved to a new territory between years. Ten (19%) of the adult males and 12 females (21%) that underwent breeding dispersal were forced to switch territories because their prior year's territory had been destroyed. In most such cases (n = 19, 86%) these sites were destroyed when new homes were built over the prior year's burrow. Among known-sex adults whose prior year's territory was intact, there were no consistent patterns that preceded territory shifts. In fact, more territory moves followed successful breeding attempts (58%, n = 43) than unsuccessful breeding attempts (42%, n = 31; Table 3), although the difference was not statistically sig-

Table 3. Circumstances associated with moves between territories by Florida burrowing owls, Cape Coral, Florida, 1988–91. Does not include moves by 10 males and 12 females after nest territories were destroyed (see text). Values in table are number of reencounters.

	Male Prior Year's Success		Female Prior Year's Success		
Circumstance	Successful	Unsuccessful	Successful	Unsuccessful	Total
Vacated territory and failed to breed	1	0	5	3	9
Moved to new burrow on same territory; prior burrow occupied by other owls	3	0	4	0	7
Mate known to have died	0	4	3	2	9
No known extenuating circumstance	10	11	17	11	49
Total	14	15	29	16	74

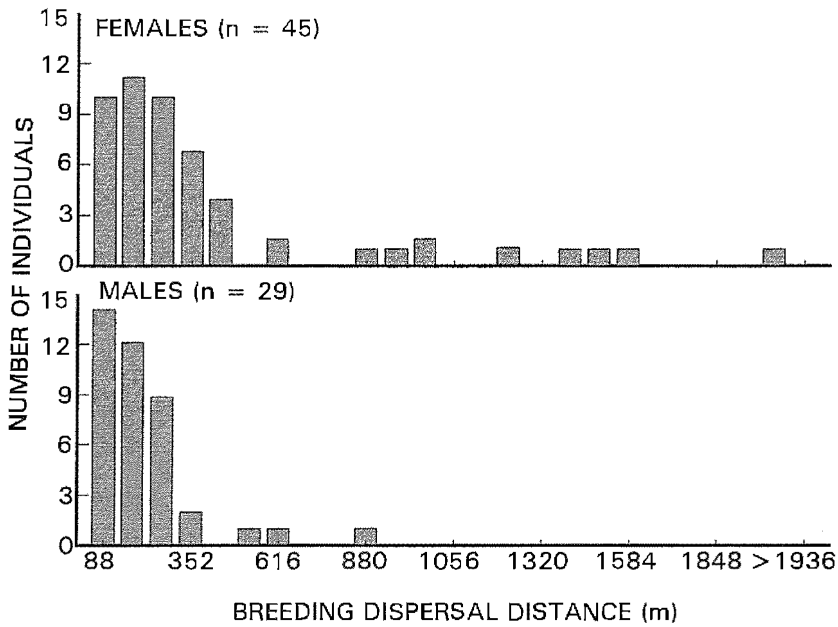

Figure 3. Histogram of breeding dispersal distances of burrowing owls from Cape Coral, Lee County, Florida, 1988–91. We defined breeding dispersal as dispersal from a previous breeding territory to a new territory or to a new burrow on the same territory if the prior year's nest burrow was occupied by another pair of breeding adults.

nificant ($\chi^2 = 1.94$, df = 1, $P > 0.1$). In 57 cases where one adult of a pair where both adults had been banded disappeared (most likely died) and where territories remained viable between years, "widowed" males remained on the same territory the next year 75% of the time (27 of 36 cases), whereas "widowed" females remained on the same territory only 33% (seven of 21 cases) of the time. This indicates that continued residency on a territory after disappearance of a mate was not independent of sex ($G = 9.66$, df = 1, $P = 0.002$).

Breeding Dispersal. From 1988–91, 29 reencountered ASY or older male burrowing owls and 45 reencountered ASY or older female burrowing owls shifted territories between years. Median breeding dispersal distance for adult males was 96 m (interquartile range = 71–220 m); median breeding dispersal distance for females was 230 m (interquartile range = 100–413 m) (Fig. 3). Breeding dispersal distance differed significantly between sexes (Mann-Whitney $U = 1422$, df = 1, $P = 0.005$).

Mate Fidelity. From 1987–90 we banded both adults of 175 breeding pairs of burrowing owls. At least one adult from 116 (66%) of these pairs was reencountered in a subsequent year. In 57 (49%) of these cases, one member of the pair was not found in any subsequent year. Of the remaining 59 cases where both pair members were known to have survived into the next breeding season, 54 (92%) pairs remained together and 5 (9%) divorced (i.e., separated and paired with other mates). Given rates of territory fidelity in our study population (Table 2), we would have expected only 61% of pairs where both adults survived to have remained together by chance.

DISCUSSION

Natal and breeding dispersal by Florida burrowing owls on our study area was strongly female biased (*sensu* Greenwood 1980). Female natal dispersal distances averaged 2.7 times those of males, and breeding dispersal distances of females averaged 2.4 times as far as for males. This conforms to the general pattern in birds (Greenwood 1980), and is consistent with findings from two Canadian burrowing owl populations (P. James this volume; J. Schmutz unpubl. data).

Among burrowing owls on our study area, territory fidelity was high in both sexes, as was mate fidelity. Some degree of territory fidelity in male burrowing owls has been observed elsewhere (Martin 1973; Haug 1985; P. James this volume). However, in the above-cited studies few burrowing owls retained the same mate between years. In an exception to this trend, Thomsen (1971) reported relatively high mate and territory fidelity among burrowing owls at Oakland, California. Thomsen's (1971) study population, like ours and unlike most others, was nonmigratory. Perhaps high mate fidelity is favored in nonmigratory burrowing owl populations and not in migratory ones.

Our study population had a high rate of male philopatry, with over one-third of all young males settling on their natal territory. In fact, the general pattern appeared to be for a young male to settle on his natal territory if his father died or underwent breeding dispersal. We also observed three cases where fathers excavated new nest burrows on their prior year's territories while their sons bred in their natal burrows 10–50 m away. At least 30% of young males that did not disperse paired with their mothers, and we suspect such matings (which were difficult to detect because only 25% of adults and 20% of young were banded each year) were more common than these data imply.

One major hypothesized function of sex-biased dispersal is avoidance of inbreeding (Greenwood and Harvey 1976, Greenwood 1980). Patterns of burrowing owl dispersal on our study area resulted in no matings between siblings, but many mother-son pairings. Our data show that following the death of a mate, females usually underwent breeding dispersal whereas males did not. Although this could be interpreted as a mechanism to promote avoidance of inbreeding in a population where natal philopatry was common, it might also reflect a premium by females on males with prior experience on a territory. For example, experienced male Eurasian sparrowhawks (*Accipiter nisus*) have been shown to have higher reproductive success than inexperienced males (Newton et al. 1981). However, the same does not always hold true for females. Pietiäinen (1988) determined that female age and experience was not reflected in increased reproductive success in a population of Ural owls (*Strix uralensis*). In our study population, if a resident male burrowing owl died following a reproductive effort producing male offspring, the widow was certain to pair with a male who was unfamiliar with that territory unless she mated with her offspring. If male familiarity with a territory influences reproductive success, it could also explain the potential discrepancy in mate fidelity between migratory and nonmigratory burrowing owl populations. In migratory populations all males may be equally unfamiliar with the current year's distribution of food and cover on their territories upon arriving in spring regardless of their tenure of residency. As a consequence, there may be little advantage in females returning to the same territory to pair with her previous mate. In a future paper we plan to explore the relationship between reproductive success and territory tenure for both male and female burrowing owls on our study area.

ACKNOWLEDGMENTS

These observations were obtained as part of a cooperative burrowing owl monitoring project by the Florida Game and Fresh Water Fish Commission and Audubon Society of Southwest Florida. The work would not have been possible without the dedicated assistance and skill of 23 Audubon Society and Lee County School System volunteers. We also gratefully acknowledge T. Wesemann and M. Rowe for freely sharing the results of their work with burrowing owls in Cape Coral with us, and for encouraging us to undertake this project. This project was funded through the Florida Nongame Wildlife Trust Fund.

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NESTING SITES AND FEEDING HABITS OF THE BURROWING OWL IN THE BIOSPHERE RESERVE OF MAPIMI, MEXICO

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ABSTRACT.—The burrowing owl (*Speotyto cunicularia*) is a threatened species throughout much of its North American distribution, yet little is known about its biology and ecological requirements in Mexico. Nest-site characteristics and feeding habits of this owl were studied over two breeding seasons in the southern Chihuahuan desert, Mexico. A significant correlation was found between nesting success and their location in *Prosopis-Hilaria* grassland "playas," where their prey consisted mainly of invertebrates (such as scorpions, coleoptera, orthoptera) and small mammals (i.e., *Dipodomys, Perognathus, Peromyscus*). Invertebrates were the most frequent prey in the owl's diet (84%), but mammals represented more than 50% of the ingested biomass in both years. The medium prey size was 7.8 ± 4.1 g in 1985 and 5.2 ± 2.5 g in 1986, the differences resulting from a higher predation on reptiles in 1985. Prey diversity was similar in both years ($H'_{1985} = 2.35$; $H'_{1986} = 2.13$), with moderate evenness ($J' = 0.6$) indicating that *S. cunicularia* in Mapimí consumes a relatively diverse array of prey species in relatively even proportions. As in other areas of America, this owl fed mainly on small prey, but some differences were noted interregionally in both the occurrence of prey and ingested biomass. These differences seem to be related to the regional differences in prey abundance and availability. Reptiles were more important in the diet of burrowing owls in Mapimi compared to other regions.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *nesting; feeding; Mapimi Reserve; Mexico; Chichuahuan Desert.*

Sitios de anidamiento y habitos alimenticios del tecolotito enano en la Reserva de la Biosfera de Mapimi, Mexico.

RESUMEN.—La información sobre la biología y requerimientos ecológicos de la lechucita de madrigueras, *Speotyto cunicularia,* es escasa o inexistente en México, aunque es una especie amenazada en la mayor parte de su distribución en Norte América. En este trabajo se presenta información sobre las características de los sitios de anidación y los hábitos alimentarios de la lechucita de madrigueras durante dos épocas reproductivas (1985, 1986) en la parte sur del desierto Chihuahuense en México. Se encontró una correlación significativa entre el éxito reproductivo y la presencia de nidos en la asociación vegetal del pastizal con *Prosopis-Hilaria.* Las presas principales de este búho fueron principalmente invertebrados (alacranes, coleópteros, ortópteros), aunque también pequeños mamíferos (roedores). Los invertebrados representaron el 80% de las presas en su dieta, pero los mamíferos le aportaron más del 50% de la biomasa consumida en ambos años. El tamaño medio de presa fue mayor en 1985 aparentemente debido a una mayor depredación de reptiles. La diversidad de presas fue similar entre años. La lechucita de madrigueras del desierto de Mapimí consume una diversidad de presas superior a la reportada para otras áreas de su distribución, representando los reptiles una mayor importancia en su dieta en relación a las otras regiones. Estas diferencias parecen relacionarse a las diferencias regionales en la abundancia y disponibilidad de presas.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl, *Speotyto cunicularia,* has a widespread distribution in grasslands throughout the Americas (Johnsgard 1988), although it is a threatened species in Canada and in some states of the U.S.A. In general, burrowing owls nest in arid, open grasslands where they prey mainly upon arthropods (primarily insects), and small mammals (Glover 1953, Coulombe 1971, Thomsen 1971, Jaksić and Marti 1981). Population declines have occurred in recent decades throughout much of the

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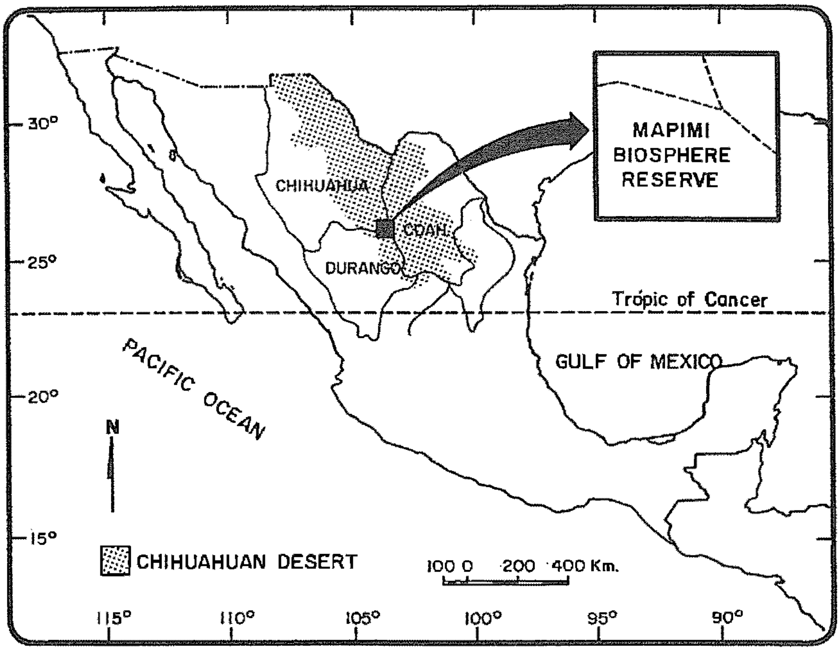

Figure 1. The Mapimí Biosphere Reserve study area.

owl's range, apparently due to habitat destruction and pest control of burrowing mammals (Best 1969, Butts 1973). This situation seems to be worsening as many contributions to this symposium have illustrated.

Very little information is available on the ecology of this species in Mexico (Rodríguez-Estrella 1993). The aim of this study is to present information on the habitat characteristics and feeding habits of the burrowing owl obtained during two breeding seasons in a northern desert of Mexico.

Study Area and Methods

The owls were observed during 1985 and 1986 in 20,000 ha of the Mapimí Biosphere Reserve in the southern portion of the Chihuahuan desert (Fig. 1). Vegetation is a xerophilus scrub dominated by *Larrea tridentata, Fouquieria splendes, Prosopis glandulosa, Jatropha dioica, Agave* sp., *Opuntia* spp. and *Hilaria mutica*. Descriptions of the area may be found in Barbault and Halffter (1981). The study area elevation ranges from 1000–1350 m. The climate is arid-tropical with a mean annual temperature of 20.8°C, a mean monthly temperature ranging from 11.8°C in winter to 28.0°C during the summer, and an annual mean precipitation of 264 mm, with about 80% of the annual precipitation occurring during the summer. Livestock grazing is the principal human activity in the area, but habitat is still in good condition.

I located owls and their burrows from March through July in 1985 and 1986. Each week I monitored every burrow which appeared to be occupied by a pair, as indicated by the fresh lining of livestock or coyote dung around the entrance. For each occupied burrow I recorded the burrow type, the surrounding vegetation type, soil texture, number of suitable perches within 40 m of the burrow, distance to permanent water, and the distance to the nearest occupied burrow. Burrow types were classified according to the animal species that constructed them. Surrounding vegetation types were classified into seven minor habitat associations dominated by different plants. Soils were classified according to texture (Table 1). A Spearman correlation analysis was performed between the burrow characteristics and nesting success to determine relevant factors. Since the young were counted only after they started to fly during the post-fledgling period, it is possible that some counts underestimated the total number of fledglings per nest. Thus, I only considered a nest to be successful when fledglings were observed around the nest. Nests received a score of 1 if they were successful, and 0 if unsuccessful.

The feeding habits of the species were determined by analyzing pellets collected in and around the nests. The remains of prey in the pellets were identified to the highest possible level of taxonomic resolution of prey categories, generally species or genus level for vertebrates, and ordinal level for invertebrates. Mean prey weights were obtained from specimens directly trapped in the field and from the Universidad Autonoma Metropolitana (UAM, Mexico) collections. Mean prey size (MPS, $\bar{x} \pm$ S.E.) was calculated according to Herrera and Jaksić (1980). Prey diversity and food-niche breadth were estimated using the Shannon (H') and Levins (B) index,

Table 1. Burrowing owl nest site characteristics at the Mapimí Biosphere Reserve. *N* is the number of total nests and ($\%_{sn}$) represents the percentage of successful nests in 1985 and 1986.

	N	$\%_{sn}$
Vegetation type		
Larrea	4	25.0
Fouquieria-Larrea	8	62.5
Larrea-Prosopis-Agave-Fouquieria	13	46.1
Prosopis-Larrea	6	33.3
Prosopis	2	50.0
Prosopis-Hilaria	17	88.2
Fouqueria-Prosopis-Larrea	2	100.0
Total	52	
Soil texture		
Clay	18	50.0
Clay-sand	27	70.4
Sand	7	57.1
Total	52	
Burrow type		
Badger (*Taxidea taxus*)	11	72.7
Fox (*Urocyon cinereoargenteus*)	11	72.7
Kangaroo rat (*Dipodomys* spp.)	20	50.0
Coyote (*Canis latrans*)	1	0.0
Desert tortoise (*Gopherus flavomarginatus*)	9	66.7
Total	52	

respectively (see Krebs 1989). Evenness was calculated as J' = H'/H'max., where H'max. equals $\log_2$ of the total prey species (Pielou 1966). The numbers of prey species were used for computation of niche breadth. The MPS between years was compared by a Student's t test. Finally, a *t*-test was used to compare prey diversity (H') between years (Hutcheson 1970, Zar 1974).

RESULTS

I found 29 nesting pairs in 1985 and 23 pairs in 1986 in the Mapimí desert region. Nesting success was similar in both years (55% in 1985 and 65% in 1986), and nest failure was mainly due to the abandonment of burrows, although predation by coyotes and badgers, and human interference occurred as well (Rodríguez-Estrella and Ortega-Rubio 1993). Of the burrows occupied in 1985, 55% were occupied again in 1986.

Vegetation type was the factor most correlated with nesting success (r_s = 0.33; P = 0.015; Spearman rank correlation coefficients). Most nests were under grassland *Prosopis-Hilaria* and *Prosopis-Larrea* vegetal associations (Table 1), and when I combined the data of both years, I found that nests located at the *Prosopis-Hilaria* grassland vegetation were the most successful. Owls used five kinds of burrows, but mainly those constructed by kangaroo rats (*Dipodomys merriami, D. nelsoni*), although some could also have been constructed by spotted ground squirrels (*Spermophilus spilosoma*) (Table 1). The occupied burrows were most frequently in clay and clay-sand soils, over 3 km from water ($\bar{x} \pm$ SD = 3806 ± 2625 m). The nests ranged between 0.03 and 4.1 km ($\bar{x} \pm$ SD = 1125 ± 1000 m) from the nearest neighboring nest and were frequently located in the lower slope of small hills (30%). The number of perches within 40 m around the nests ranged from 4–20 ($\bar{x} \pm$ SD = 11.8 ± 4.9) (Rodríguez-Estrella and Ortega-Rubio 1993).

A total of 184 and 111 pellets were analyzed in 1985 and 1986, respectively. Burrowing owls in Mapimí preyed upon a wide variety of invertebrates, mainly scorpions, arachnida, coleoptera, and orthoptera preys (Table 2, Appendix 1) as well as small mammals (*Dipodomys, Perognathus, Peromyscus*). The proportions of the groups (mammals, birds, reptiles and invertebrates) in the diet of this owl were different between the two years (χ^2 = 19.2; df = 3; $P < 0.01$) as was the ingested biomass for each group (χ^2 = 979.0; df = 3; $P < 0.01$). Despite the greater proportion of invertebrates in the diet (85%), mammals represented >50% of the ingested biomass in both years. The MPS was different between the years (t = 20.01; df = 3541; $P < 0.01$; Table 2), due to a higher predation on reptiles in 1985. The mean number of prey per pellet was not different between years (t = 0.07; df = 293; $P > 0.05$; Table 2). Trophic diversity (H') was similar in both years (t = 1.14; df = 197; $P >$ 0.05), showing a relatively high prey diversity, but moderate evenness (J') (Table 2). The moderate evenness values indicate that *S. cunicularia* in Mapimí consume a relatively diverse array of prey species in relatively even proportions.

DISCUSSION

In the Mapimí desert, the burrowing owl is a common resident species throughout the year. In this region, they nest in open grassland habitats called "playas," much as they do in other North American deserts. They particularly nested where elevated perches were available and where their nests were mainly associated with a mixture of grassland vegetation and sparse trees (Rodríguez-Estrella and Ortega-Rubio 1993).

Table 2. Feeding habits of burrowing owls in Mapimí, Mexico. %P = percentage of the total number of prey; %B = percentage of the total ingested biomass (see Appendix 1).

	1985		1986	
PREY	%P	%B	%P	%B
Mammals	8.9	52.9	8.6	50.9
Birds	1.1	6.3	2.8	18.2
Reptiles	4.6	27.1	3.2	12.2
Invertebrates	85.5	13.7	85.4	18.7
Total number of prey & biomass[a]	2350	12 179.3	1193	5542.1
No. of pellets	184		111	
H′	2.35		2.13	
J	0.61		0.62	
B	8.03		5.45	
No. prey species	59		48	
No. pf prey/pellet	11.9 ± 11.4		11.8 ± 6.9	
MPS[a]	7.8 ± 4.1		5.2 ± 2.5	

[a] Biomass is given in grams.

The tendency of owls to nest in "playas" with the *Prosopis-Hilaria* association seems to be enhanced by the high availability of burrows, fine soil texture (clay-sand), number of perches, low nest predation, and availability of prey. All these factors may improve the reproductive success of burrowing owls in the *Prosopis-Hilaria* association (Rodríguez-Estrella and Ortega-Rubio 1993).

Burrowing owls in Mapimí used four types of mammal burrows as well as desert tortoise (*Gopherus flavomarginatus*) burrows. Frequently, these burrows were located in the lower portion of small hills where they offered a good horizontal visibility to the owl, possibly to avoid predation by mammals (Green and Anthony 1989, 1993).

At Mapimí a clay-sand soil texture seems to be the principal factor influencing burrow reuse, probably because it increases the longevity of a burrow (Morafka et al. 1981, Rodríguez-Estrella 1993). However, burrow reuse in Mapimí may also be related to low nest predation and to successful breeding in the previous year (or years). In this case, fourteen of 21 successful nest-burrows in 1985 were reused in 1986.

The prey of burrowing owls in Mapimí consisted mainly of insects and small mammals, similar to their diet in other areas (Coulombe 1971, Thomsen 1971, Jaksić and Marti 1981, Johnsgard 1988). These prey were especially abundant in the *Prosopis-Hilaria* association (Grenot and Serrano 1981, Thiollay 1981, Rodríguez-Estrella 1993).

The proportion of prey at the class level in Mapimí is similar to the diet of *Speotyto* in other areas of the U.S.A. (Fig. 2). As in other areas, this owl fed mainly on small prey. By numbers, invertebrates are the most common prey in all regions, but vertebrate prey are the most important prey in terms of biomass. However, some differences were noted between regions in both the occurrence of prey and ingested biomass. For example, in California, the occurrence of mammals in the diet of *Speotyto* appears to be more important than in other regions (Fig. 2a), but in terms of biomass, mammals were more important in Colorado (Fig. 2b). Reptiles were more important in the diet of burrowing owls in Mapimí compared to other regions (Fig. 2b) and its diet showed the highest reported prey diversity (H′) throughout its distribution (see Thomsen 1971, Jaksić and Marti 1981). The differences in the diet between regions seem to be related to regional differences in prey abundance and availability (Marti 1974, Jaksić and Marti 1981, Rodríguez-Estrella 1993).

Results of this work may lend support to the hypothesis that general features of predation by vertebrates exist in hot arid environments. Donázar et al. (1989) found that the diet of the great horned owl *Bubo virginianus* in North American deserts was related mainly to the presence of reptiles and arthropods. Hernández et al. (1994) concluded that the major role of reptiles and invertebrates as prey in the diet of coyotes (*Canis latrans*) in arid eco-

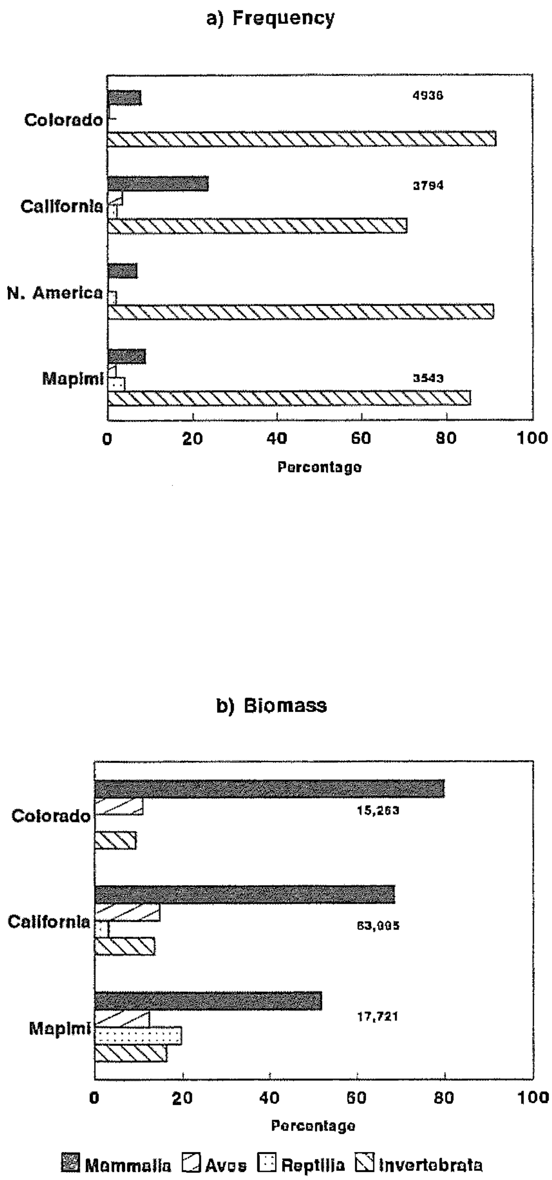

Figure 2. Percentage of prey categories in the diet of *Speotyto* in Colorado (Marti 1974), California (Thomsen 1971), North America (Johnsgard 1988) and Mapimí (this study). The numbers over the bars indicate (a) the total number of prey and (b) the total biomass in grams.

systems may be a characteristic feature of their trophic webs because of the high species density and abundance of these groups resulting from increased insolation. My results indicate similar trends in the use of reptiles and arthropods by the burrowing owl in the hot desert of Mapimí.

Cattle raising is one of the potential causes for the loss of burrows for the owl (Howie 1980), and in Mapimí, this human activity is the most important economic activity. During the study I observed several burrows destroyed by cattle. Thus, studies on the effects of cattle density on the breeding success of the burrowing owl should be conducted in order to determine the real effect of this activity on the owl population.

Finally, important changes in land use are expected over the next few years in many parts of Mexico as a result of the recent Trade Agreement (NAFTA) between Mexico, Canada and the U.S.A. The NAFTA will surely pressure a change in natural resource management in Mexico; i.e., the practices of the cattle industry. Thus, management plans should consider competitive economic practices with the least biological effects to ensure the conservation of Mexico's natural resources.

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Appendix 1. Burrowing owl diet in the Biosphere Reserve of Mapimí, Durango, Mexico in 1985 and 1986. The totals show the number of individuals per group and the ingested biomass in grams.

	WEIGHT	1985		1986	
	(g)	% FREQ.	% BIOM.	% FREQ.	% BIOM.
Mammalia					
Lepus californicus juv.	300	0.30	17.24	—	—
Sylvilagus audubonii juv.	300	—	—	0.18	10.83
Spermophilus spilosoma					
adult	95	0.38	7.02	0.18	3.43
juvenile[a]	50	0.76	5.50	0.81	6.50
Thomomys umbrinus					
litter	40	0.09	0.66	—	—
Dipodomys merriami					
adult	37	0.21	1.52	0.45	3.43
juvenile	18.5	0.51	1.22	0.09	0.33
Dipodomys nelsoni					
adult	80	0.04	0.66	—	—
juvenile	40	—	—	0.09	0.72
Dipodomys sp.					
adult	40	—	—	0.45	3.61
juvenile	20	—	—	0.18	0.72
Perognathus penicillatus					
adult	15	1.62	4.68	1.17	3.52
juvenile[a]	10	0.13	0.16	0.99	1.17
Perognathus baileyi	15	0.09	0.25	0.27	0.81
Perognathus spp.					
adult	12	0.26	0.62	0.45	1.35
juvenile[a]	5	0.13	0.16	0.09	0.09
Neotoma albigula juvenile	90	—	—	0.09	1.6
Onychomyis torridus	14.5	0.13	0.36	—	—
Peromyscus eremicus					
adult	20	0.68	2.63	1.26	5.05
juvenile[a]	10	0.26	0.44	0.18	0.30
Reithrodontomys megalotis					
adult	15	0.30	0.86	0.36	1.08
Sigmodon hispidus					
juvenile	55	0.13	1.35	—	—
Mus musculus					
adult	18	0.68	2.36	—	—
juvenile[a]	9	0.04	0.04	—	—
Rodentia, unidentified					
adult	18	1.57	4.43	1.53	5.52
litter	5	0.09	0.10	0.36	0.36
Total[b]		208	6439.7	103	2821.1
Aves					
Callipepla squamata	189	—	—	0.09	3.41
Zenaida asiatica	152	—	—	0.09	2.74
Caprimulgidae	57	0.04	0.47	—	—
Myiarchus tyrannulus	27	0.04	0.47	0.09	0.49
Campylorhynchus brunneicapillus	50	0.90	0.66	—	—
Mimus polyglottos	53	0.17	1.36	—	—
Toxostoma curvirostre	50	—	—	0.09	0.90
Polioptila melanura	8	0.04	0.07	—	—

Appendix 1. Continued.

	WEIGHT (g)	1985		1986	
		% FREQ.	% BIOM.	% FREQ.	% BIOM.
Carpodacus mexicanus	21	0.04	0.17	—	—
Unidentified	20	0.55	2.13	2.61	10.65
Unidentified	50–100	0.09	1.23	—	—
Total		25	769	33	1008
Reptilia					
Scaphiopus couchi	17	0.34	1.12	0.63	2.15
Cophosaurus texanus	20	0.13	1.23	0.09	0.90
Holbrookia maculata	20	0.13	1.23	—	—
Scleoporus undulatus	10	1.32	2.55	1.44	2.89
Phrynosoma cornutum	36	0.72	5.02	0.18	1.30
Cnemidophorus inornatus	15	0.55	5.34	—	—
Cnemidophorus scalaris	20	0.26	2.46	0.09	0.90
Unidentified lizards	15	0.04	0.12	—	—
Masticophis sp.[c]	300	0.43	3.69	0.45	1.89
Pituophis melanoleucus[c]	280	0.17	1.31	0.18	0.72
Unidentified snakes	20	—	—	0.36	1.44
Unidentified snakes	100	0.09	1.23	—	—
Total		109	3303	38	676
Invertebrata					
Scorpionida	2	6.68	2.58	8.65	3.46
Arachnida	1	4.68	0.90	7.39	1.48
Solifugae	1	3.11	0.60	4.23	0.85
Chilopoda	5.0	0.21	0.21	—	—
Coleoptera	0.5	3.45	0.33	7.48	0.75
Meloidae	0.5	0.04	tr	0.09	0.01
Carabidae	0.5	1.11	0.11	4.23	0.42
Scarabaeidae	0.5	6.51	0.63	4.68	0.47
Phyllophaga	0.5	1.96	0.19	8.20	0.82
Diplotaxis	0.5	0.17	0.02	0.27	0.03
Elateridae	0.5	0.04	tr	0.18	0.03
Tenebrionidae	0.5	2.26	0.22	0.27	0.03
Curculionidae	0.5	0.38	0.04	0.81	0.08
Orthoptera	1.5	0.04	0.01	—	—
Gryllidae	1	17.02	3.28	30.45	6.10
Acrididae	2	5.23	2.02	2.97	1.19
Phasmatodea	1	0.17	0.03	0.09	0.02
Formicidae	—	27.70	0.53	6.58	tr
Hymenoptera	1	1.91	0.37	0.27	0.05
Vespidae	4	2.21	1.43	3.15	2.53
Dermoptera	2	0.13	0.05	0.27	0.11
Lepidoptera	1	—	—	0.09	0.02
Unidentified	1	0.26	0.05	1.44	0.29
Total		2008	1667.6	1019	1037.0
Grand Total		2350	12 179.3	1193	5542.1

[a] Including litter of the prey.
[b] Totals represent the number of prey and the biomass (g) for each animal class.
[c] Individuals of different weights (20, 30, 60, 100 g).

MANAGEMENT AND RELATED SUBJECTS

J. Raptor Res. Report 9:107–111

RECOVERY PLAN FOR THE BURROWING OWL IN CANADA

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ABSTRACT.—The population of burrowing owls, *Speotyto cunicularia,* nesting in Canada has been in decline since the mid-1900s and was classed as Threatened in 1978. The burrowing owl was extirpated from British Columbia, where it is now being reintroduced, and has experienced major declines across Manitoba, Saskatchewan, and Alberta. Habitat loss is considered a significant cause of decline although increased mortality from pesticides, vehicle collisions and unknown causes, (including mortality outside of Canada on migration and winter areas) are also of concern. Low productivity may also be contributing to the population decline. A National Recovery Plan for the burrowing owl, approved in December 1992, included these seven major strategies: Reduce mortality on the breeding grounds, increase productivity, protect and manage nesting habitat, monitor populations, manage migration and wintering areas, conduct release programs, and develop public support.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *Canada; Recovery Plan.*

Plan de recuperacion del tecolotito enano en Canada

RESUMEN.—La poblacion de tecolotito enano, *Speotyto cunicularia* que anida en Canada a disminuido desde mediados de los 1900s y se clasifico como amenazado en 1978. El tecolotito enano se extirpo de British Columbia donde actualmente se trata de reintroducir, y ha sufrido grandes bajas atraves de Manitoba, Saskatchewan y Alberta. Perdida del habitat se considera una causa significante en las bajas, aunque aumento en la mortlidad a causa de pesticidas, choques con vehiculos y causas no conocidas (incluyendo mortalidad fuera de Canada en migracion y areas invernales) tambien son de considerar. Baja productividad tambien puede estar contribuyendo a las bajas de la poblacion. Un plan nacional de recuperacion para el tecolotito enano aprobado en diciembre de 1992 incluyo estas siete estrategias: Reducir mortalidad en areas de reproduccion, aumentar la productividad, proteger y manejar el habitat de anidacion, monitorear las poblaciones, manejar areas de migracion e invernacion, realizar programas de liberacion, y desarrollar apoyo publico.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl, *Speotyto cunicularia,* has been classed as a Threatened species in Canada since 1978. Canada appointed a National Burrowing Owl Recovery Team in 1989 and the National Recovery Plan for the Burrowing Owl (Haug et al. 1992) was approved in December 1992. With this paper, I briefly explain the burrowing owl's status in Canada, the reasons for its decline, and the recovery actions proposed in the recovery plan. I also stress that this migratory species spends six months outside of Canada. The species recovery in Canada therefore depends on international cooperation.

STATUS OF THE BURROWING OWL IN CANADA

The burrowing owl is found in the four western provinces of Canada: Manitoba, Saskatchewan, Alberta and British Columbia. Our most western population, in the interior valleys of British Columbia, had been extirpated, but a release program reestablished a small population, six pair in 1992 (Haug et al. 1992).

Our second population, estimated at about 2000 pairs (Haug et al. 1992) occupies the Canadian prairies from Alberta to Manitoba. Figure 1 shows that the range has contracted, especially on the eastern side, since 1978.

Our concern for the survival of this species arises from several studies which show precipitous declines in the population. James (1992a) reported declines of approximately 10% per year on his study area near Regina. Less than 10% of sites in the Saskatoon area occupied by burrowing owls in

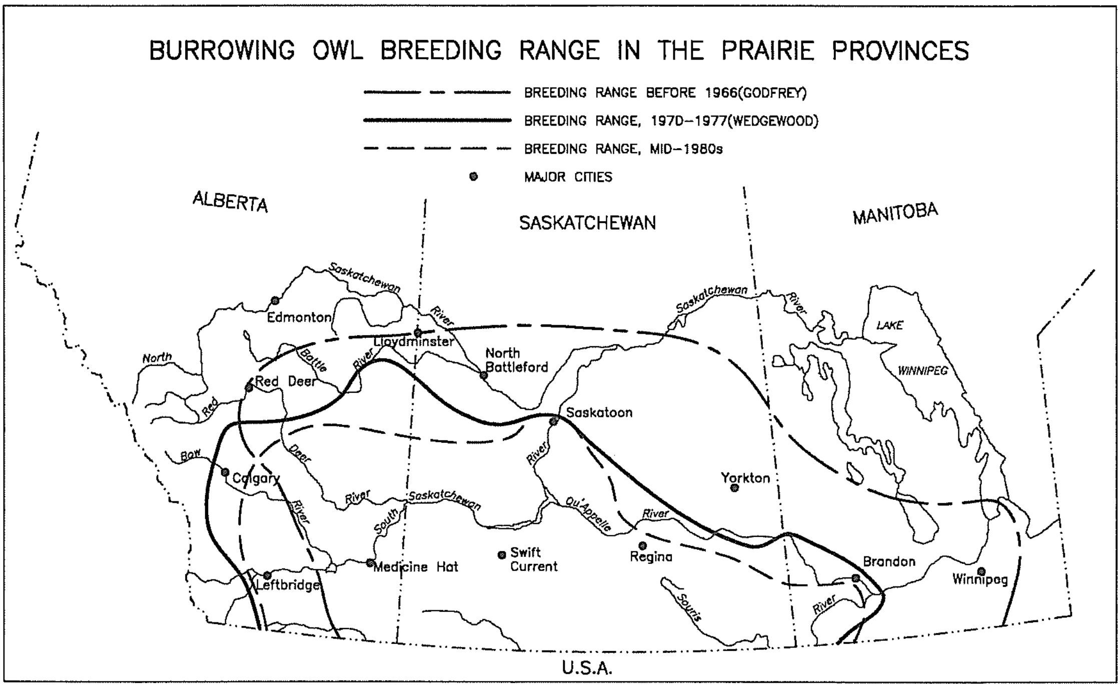

Figure 1. Burrowing owl breeding range in prairie Canada after Bjorklund (1992).

1975 (Wedgwood 1976) were still occupied by burrowing owls in 1992 (Wedgwood pers. comm.). The number of pairs reported breeding on Operation Burrowing Owl sites declined steadily from 721 in 1988 to 322 in 1993 (Dundas 1993). The Operation Burrowing Owl data is obtained by rechecking initially occupied sites and obtaining reports of new sites. Rechecking same sites creates a bias toward showing a decline (Rich 1984). However, if the observed population decline is simply due to movement between sites, a substantial number of new sites should be reported each year and old sites should eventually be reoccupied. That this is not occurring indicates the decline is real (Hjertaas 1992). In Manitoba the population has declined from 76 pairs in 1982 (Ratcliff 1986) to 28 pairs this year and the range has contracted into the southwest corner of the province (Haug et al. 1992).

Cause of the Decline. The causes of the decline are complex and interrelated. The National Recovery Team has identified loss, fragmentation and degradation of breeding habitat, mortality from collisions with vehicles, exposure to the pesticide carbofuran, and reduced productivity as contributing factors (Haug et al. 1992). Canadian burrowing owls may also experience problems on migration and wintering areas.

The Recovery Plan. The recovery goal is "To increase populations of the burrowing owl in Canada to a self-sustaining level such that the species is no longer considered Threatened or Endangered." This goal is elaborated in two objectives: to produce a stable or increasing population of more than 3000 pairs in the prairie provinces and to establish a viable population in British Columbia. Seven principal strategies were adopted to meet these objectives (Haug et al. 1992).

1. Reduce mortality on the breeding grounds

The principal mortality factors affecting burrowing owls include pesticide poisoning, collisions with vehicles, predation and occasional incidents such as shooting. A major strategy is to eliminate the negative effects of pesticides on burrowing owls. Although all pesticides, including rodenticides, are of concern, carbofuran is of greatest concern. Carbofuran is widely used in prairie Canada for grasshopper control, and its impacts on burrowing owls and their productivity when applied within 250 m of the nest burrow have been demonstrated (James and Fox 1987). Agriculture Canada has responded to this concern by imposing an interim label restriction preventing carbofuran application within 250 m of burrowing owl burrows while a final decision on relicensing carbofuran is pending. The effectiveness of this label is in doubt as many farmers are not aware of the restriction (Mufatov 1992).

Additional planned action is aimed at reducing collisions with vehicles, publicity and enforcement to prevent shooting, developing policy to resolve owl-human conflicts and research and monitoring of mortality rates and causes.

2. Increase productivity

Increasing productivity could help stabilize or increase the burrowing owl population. Research on nest predators, causes of differential productivity between areas, and the effect of food supplies on productivity is planned or underway.

Research conducted during 1992 suggests that food is limiting productivity (Wellicome 1992) and that habitat management to increase food supplies may be necessary to boost productivity in some areas. Food may be limiting because nests are commonly situated in heavily grazed pastures surrounded by intensively cultivated land. Neither of these habitats supports large numbers of microtines, a key food resource during the earlier parts of the breeding season.

3. Protect and manage nesting habitat

Unfortunately burrowing owls on the prairies tend to select potentially arable grasslands as nest sites. With the decline of the mixed farm and trend toward pure grain farming, nesting habitat has disappeared, leaving only small and fragmented habitats for the owls (Haug 1985, Hjertaas and Lyon 1987, Haug and Churchward unpubl. data). This fragmentation may increase predation and create other problems, such as the lack of foraging habitat just discussed.

The Recovery Plan calls for a series of actions to maintain critical nesting areas and essential habitat features such as nesting holes and foraging areas. The emphasis has been on landowner contact programs such as Operation Burrowing Owl. These programs are designed to create awareness and protect privately owned nesting areas (Hjertaas 1992) and will continue as part of an expanded effort to identify and protect critical nesting areas.

Many provincial and federal agricultural policies directly encourage and subsidize conversion of grassland to cultivation, thus reducing habitat available for burrowing owls and other species. The plan identifies this as a basic and urgent problem which must be resolved. Unfortunately, identifying the problems with these policies is easier than achieving a consensus for change.

The Recovery Plan identifies the need to expand from simple habitat protection to habitat management to ensure sites have the necessary habitat components, including adequate nest burrows and feeding areas.

4. Monitor populations

Assessing the effectiveness of any plan requires checking results against the goals and objectives. Monitoring actual population size across the prairies would be very expensive because the burrowing owl population is thinly spread over large areas. While a better understanding of habitat may eventually facilitate such surveys, the key to recovery on the prairies is a stable or increasing population. Except in British Columbia and Manitoba, where near total counts are feasible, monitoring will therefore focus on trend, mortality and productivity rather than on absolute numbers. Randomly chosen monitoring blocks have been established in Alberta and Saskatchewan to aid in tracking population changes.

5. Manage on migration and wintering areas

The winter range and migratory corridors of Canadian burrowing owls are not known. James (1992b) suggests the lack of band returns during winter indicates the prairie population migrates to Mexico. Band returns from the migration period (Fig. 2) indicate movement that could stop in the United States or continue into Mexico.

The importance of winter range to survival of the population makes locating and managing the winter range a key part of recovery. Continued banding studies, banding on wintering areas, and techniques such as genetic or chemical analysis or radiotelemetry will be used to identify wintering areas of Canadian burrowing owls. This work will be combined with surveys of possible wintering areas, especially in Mexico, to determine winter distribution of the burrowing owl.

The ecology and factors limiting survival of the burrowing owl during the migration and winter must also be determined. This work can proceed

Figure 2. Foreign recoveries of burrowing owls banded in Canada (modified from James 1992b) showing banding and recovery sites. Numbers indicate the month of recovery.

immediately. Even if research areas are not ultimately proven to harbor burrowing owls from Canada, the information gained will be useful in managing resident and other migratory populations.

Identifying migration and winter areas and studying the species during this period must be conducted cooperatively. If this research identifies substantial management problems, management to help the burrowing owl should also be cooperative. This approach could mean joint projects between members of our team and Mexican or American researchers. It may involve naming Mexican and American representatives to the Canadian Recovery Team. The Recovery Team is currently seeking possible partners for winter studies.

6. Conduct releases

Where populations of burrowing owls are very low, as in Manitoba, or absent, as was the case in British Columbia, releases offer what may be the only way to maintain or establish breeding populations.

7. Develop public support through education

Public awareness is even more essential for recovery of the burrowing owl than for many other threatened species because the species has frequent public contact. Nesting in intensively farmed areas, in towns and cities, and on private land makes it vulnerable to human interference, land use changes and pesticides. Actions necessary to help the burrowing owl recover will depend primarily on public goodwill and cooperation. Planned communication will promote specific programs and increase awareness of the burrowing owl. It will also address underlying issues in an attempt to communicate that problems with the burrowing owl are not unique, but symptomatic of our land use practices and general environmental degradation. As such, they cannot be dealt with in isolation, but as part of the larger realm of public policy.

CONCLUSION

In spite of recovery efforts, population declines are continuing, increasing our concern for this species. We will be actively implementing the plan and attempting to address the above issues.

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OPERATION BURROWING OWL IN SASKATCHEWAN

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ABSTRACT.—Operation Burrowing Owl was initiated in 1987 as a private stewardship program to protect burrowing owl, *Speotyto cunicularia*, habitat. Landowners with burrowing owls were asked to sign a voluntary agreement to preserve the nesting site for five years and to annually report the number of owls at the site. In return they would receive a gate sign and an annual newsletter. Eighty-five percent of eligible landowners did enroll when contacted. After five years 499 landowners had agreed to maintain a total of 16 000 hectares of grassland as burrowing owl nesting habitat. Numbers known to be nesting on these sites fluctuated from 721 in 1988 to 322 in 1993. Operation Burrowing Owl has protected habitat and substantially raised public awareness of the burrowing owl. Data collected through the program indicate a significant population decline is occurring. Other available data sources also indicate that populations declined since 1988.

KEY WORDS: *burrowing owl; Operation Burrowing Owl;* Speotyto cunicularia; *Canada; management; habitat; Saskatchewan.*

Operacion tecolotito enano en Saskatchewan

RESUMEN.—Operacion Tecolotito Enano fue iniciada en 1987 como un programa privado de administracion para proteger el habitat del tecolotito enano, *Speotyto cunicularia*. A terratenientes con tecolotito enano se les pidio firmaran un acuerdo voluntario para preservar el habitat de anidacion por 5 años y que anualmente reportaran el numero de tecolotes en el sitio. A cambio recibirian un anuncio para puerta y un boletin informativo anual. 85% de los terratenientes habian acordado mantener un total de 16 000 hectareas de pradera como habitat reproductivo des tecolotito enano. Numeros que anidaron en estos sitios variaron de 721 en 1988 a 322 en 1993. La Operacion Tecolotito Enano ha protegido habitat y ha elevado la conciencia publica sobre el tecolotito enano. Datos colectados durante el programa indican que una disminucion significante ha occurrido en la poblacion. Otras fuentes de informacion tambien indican que las poblaciones han disminuido desde 1988.

[Traducción de Filepe Chavez-Ramirez]

The majority of the arable land in Canada's prairie provinces is privately owned. Thus conservation initiatives in this landscape are largely dependent on cooperation between landowners and conservationists. One such cooperative program, Operation Burrowing Owl (OBO), operated in Saskatchewan since 1987 and now also operates in Alberta to protect privately-held grasslands used as nesting areas by the burrowing owl, a threatened species in Canada.

The need for a habitat protection program for the burrowing owl was demonstrated when Hjertaas and Lyon (1987) found that twenty-one percent of the grassland areas in southeastern Saskatchewan identified as potential burrowing owl nesting habitat had been cultivated or otherwise eliminated over the previous seven years.

Hjertaas and Lyon (1987) also learned that the burrowing owl was relatively rare: burrowing owls were located on only 13 of 703 grassland plots searched. However, comments from farmers whose land we searched suggested the burrowing owl had formerly been more common. Discussions with farmers also showed that most could identify a burrowing owl, but very few knew it was threatened or even uncommon.

In 1986 thirteen pairs of burrowing owls near Kronau, Saskatchewan, were threatened by the landowner's decision to cultivate the pasture they nested in. This colony was saved when the World Wildlife Fund (Canada) and the Saskatchewan Wildlife Federation agreed to pay the landowner $360.00 annually to retain the area as pastureland.

The above 1986 survey and the threat to the Kronau colony demonstrated an urgent need for a program to protect burrowing owl habitat. They also showed the potential for a cooperative program to raise awareness of the burrowing owls' threatened status and to be an effective conservation force. In 1987, OBO was initiated as a joint project of the Saskatchewan Natural History Society, Saskatchewan Wildlife Federation, World Wildlife Fund, Wildlife Habitat Canada and Saskatchewan Environment and Resource Management with the following objectives: (1) to protect burrowing owl habitat by publicly recognizing the landowners' role in providing habitat; (2) to survey burrowing owl populations across Saskatchewan and estimate provincial and regional populations; (3) to increase public awareness that the burrowing owl is a threatened species; (4) to establish a method for annual census of the owl population on protected habitat; and (5) to facilitate research.

METHODS

The core of OBO is a one-page volunteer agreement which OBO staff discuss and sign with landowners who have burrowing owls on their property. The OBO partners agree to provide the landowner with an OBO sign (with the landowners name), which is designed to be placed at the farm gate, and an annual newsletter about burrowing owls. The participating landowners agree not to cultivate the described nesting area for the five-year term of the agreement and to report the number of pairs of burrowing owls annually when requested to do so. This agreement is essentially a handshake agreement which can be cancelled at any time and is not legally enforceable.

At the start of this program the location of the majority of our burrowing owl colonies was unknown. Thus, to meet the objectives of raising awareness and surveying populations, and also to find landowners with whom we could sign agreements, we initiated a publicity program. Our key message was ". . . the burrowing owl is a threatened species which needs help. If you know where they nest please tell us." This message was initially sent to every rural post office box holder within the burrowing owl's Saskatchewan territory with a simple mail-back questionnaire.

The initiation of OBO received a substantial boost from the International President of the World Wide Fund For Nature, His Royal Highness Prince Philip, who participated in a formal initiation of the program. Eight landowners from across the province were enrolled in the program and received their OBO signs from the Prince. In addition to excellent coverage in the provincial media, almost every one of the widely read rural weekly papers ran the OBO story on their front page, using photographs provided by OBO of someone from their region with H.R.H. Prince Philip. In 1992 the Prince again assisted the program by writing a thank-you letter to renewing members.

Since the 1987 initiation we have attempted to keep OBO in the pubic eye through the use of a brochure, by giving presentations to schools and groups and by placing occasional stories in the media. A toll free "HOOT LINE" was introduced in 1991 to allow people to report sightings or census results at no cost to themselves.

Ongoing contact with the cooperating landowners via the OBO Newsletter and the owl population survey is an important part of OBO. This contact has three purposes: (1) to reinforce the message that the burrowing owl is threatened and maintenance of nesting sites is vital; (2) to obtain population data annually; and (3) to provide information on safer practices (e.g., on the use of pesticides). Personal contact and inspection of the nesting areas by OBO staff occurred primarily at the sign-up and again, after 5 years, when the agreements were renewed. Landowners appeared to take pride in showing OBO staff their burrowing owl site and usually enrolled immediately. Occasionally, personal contact could not be made and contacts with the landowner were limited to mail and telephone. Such contacts were less successful in enrolling members than personal contacts.

Nest boxes for burrowing owls were placed on a series of OBO sites. Experience has shown that, except for special situations like golf courses, adequate natural holes were available for nesting on most OBO sites, but nest boxes were valuable in increasing landowner interest, encouraging owls to nest in safer areas, (such as at the edge instead of on a ball diamond) and in facilitating banding and other research.

RESULTS

OBO staff noted a dramatic increase in awareness of the burrowing owl as a threatened species following the mailing to landowners and the widespread media coverage of H.R.H. Prince Philip inaugurating the program. The OBO intent, that people who had burrowing owls would value them as something special, was achieved in many cases. This change in awareness and attitude was very noticeable during contacts to enroll landowners. The OBO gate signs (which 75% of members have erected) and the continuing publicity by OBO as well as promotion by the landowners themselves, have helped maintain awareness of the burrowing owl since 1987. Nonetheless, some landowners remain unfamiliar with the program: in 1992 82% were familiar with the burrowing owl while only 62% reported familiarity with Operation Burrowing Owl.

During the initial five years, 499 landowners, ranging from individual farmers to the city of Moose Jaw, enrolled 16 000 ha of grassland nesting habitat in OBO. Eighty-five percent of the landowners, who had burrowing owls and were eligible for the program, did enroll when contacted. The remaining 15% were either not interested in burrowing owls or did not want to become involved in what they perceived as another government program.

Beginning in 1992, we sought to re-enroll the landowners whose 5-year agreements were expiring. Two hundred and eighty-six of the 356 members did enroll for an additional 5 years even though only 46% of them still had burrowing owls nesting on their property. Those who no longer had burrowing owls were convinced that keeping the habitat is essential to hopes for a recovery in the population. New agreements have just balanced dropouts and maintained the membership in 1993 at the 499 achieved in 1991.

Data collected during the 1993 census of the burrowing owl on OBO sites indicated that the grassland habitat originally enrolled in the program remained on 98.1% of sites although cessation of grazing may have reduced the attractiveness of 6.8% of the sites to nesting burrowing owls (Dundas 1993). Only 1.9% of landowners had already or were planning to cultivate areas enrolled in OBO. No direct comparison with this rate of loss of grassland habitat is available. However, data from the national census show 3.76% of the "unimproved" land (i.e., native ecosystem) in agricultural Saskatchewan was "improved" for agriculture between 1986 and 1991 (Ted Weins pers. comm.). Improved for agriculture usually means cultivated. Because much of the "unimproved land" in agricultural Saskatchewan is not suitable for cultivation, the rate of conversion on potentially arable lands, which includes almost all OBO sites, would have been significantly higher than 3.65%. This suggests that OBO is having a positive affect on maintenance of burrowing owl habitat. OBO has given us a list of known nesting areas and a known minimum population size, but the accuracy of provincial population estimates is limited by the unknown number of unreported sites.

The trend in population numbers is perhaps more important than the absolute number of burrowing owls. The annual reports from landowners have provided an opportunity to track the population trend. Unfortunately, this method of collecting data creates possible biases from count accuracy, low reporting rates and annual movement of owls.

We believe the count accuracy is reasonable for small colonies. Only a small number of sites supported more than five pairs of nesting owls where landowners may be confused about the number of pairs. For example, Table 1 shows that in 1992 the most common nesting situation was a single pair, with more than half the population in colonies of one, two or three pairs. We have attempted to verify larger colony counts by personal visits.

Table 1. Size of burrowing owl colonies on Saskatchewan Operation Burrowing Owl sites in 1992 with total number and percentage of pairs inhabiting colonies of each size (modified from Bjorklund 1992).

No. of Pairs in Colony	No. of Colonies	Total No. of Pairs	% of All Pairs
1	112	112	20.9
2	56	112	20.9
3	20	60	11.2
4	19	76	14.1
5	9	45	8.4
6	6	36	6.7
7	4	28	5.2
9	1	9	1.7
10	1	10	1.8
14	2	28	5.2
21	1	21	3.9

A second bias is created because not all members responded to questionnaires on population numbers in 1988, 1989 and 1990. In 1991 a policy of telephoning to obtain late reports, better designed and postage-free reporting cards and a draw for gift certificates for reporting members produced reporting rates of 95% or greater. The lower response rates for those three years probably lowered the total number of owls reported and may bias the number of owls per member upward since participants who had owls may be more likely to submit survey reports.

The final possible bias in the OBO data set arises because it starts with known occupied habitats. Rich (1984) showed there was enough movement between burrows that simply rechecking used burrows is inadequate to monitor populations. Although the Operation Burrowing Owl data is based on blocks of land, usually pastures rather than individual burrows, some bias should exist. Thus, a decline is expected on existing sites even if the provincial population is stable.

The number of owls reported from OBO sites has declined substantially (Table 2) since 1991 while the number of pairs per reporting member has declined since 1988.

If the population is stable the decline in owl numbers at previously occupied sites should be at least partially offset by new enrollments and abandoned sites should be reoccupied after a period of time (Rich 1984). If only half of the 62% of landowners familiar with OBO reported new sites, one

Table 2. The number of pairs of burrowing owls reported by Operation Burrowing Owl (OBO) members, the number of members from whom reports were received and an index of pairs per reporting member from 1987 to 1993 (Dundas 1993).

	No. Owl Pairs	No. Members Responding	OBO Pair Index
1987	600	265	2.26
1988	721	232	3.11
1989	657	221	2.97
1990	467	265	1.76
1991	647	497	1.30
1992	561	482	1.16
1993	322	473	0.68

third of all new sites in the province would be reported. Actual reporting rates should be higher, because people do report burrowing owls they observe on other peoples' land, and landowners who are unfamiliar with Operation Burrowing Owl may nonetheless know the burrowing owl is threatened and report observations to conservation officers. However, in 1993, when the reported population on existing sites declined by 239 pairs, only 11 new members were enrolled. In addition, almost all abandoned OBO sites are remaining unoccupied.

The other data sources available all confirm the population decline shown by OBO. The population on Paul James' study area near Regina has declined from 78 pairs in 1987 to 18 pairs in 1993 (Paul James pers. comm.). Naturalists at Saskatoon report that they can no longer find hurrowing owls near that city (Stan Shadick pers. comm.), and other naturalists have also noted declines.

More traditional randomized surveys to confirm the population status and trend have been difficult and expensive. In 1994, Saskatchewan Environment and Resource Management employees attempted to address the issue of bias by establishing randomly selected population monitoring blocks in suitable habitats. Thirty-four days of search effort discovered three pairs of burrowing owls (Earl Wiltse pers. comm.). A survey which would produce statistically valid numbers would clearly be very expensive.

Conclusion

A private stewardship program such as OBO has limitations, but has been successful in creating awareness and enlisting broad support for burrowing owl conservation. Most importantly, it has established a network of cooperative and concerned landowners who are willing to retain and, in some cases, even manage grassland habitat for burrowing owls. The vast majority of landowners honored their agreements and maintained the nesting habitat even if the owls were no longer present. General public awareness of the burrowing owl has increased dramatically since 1987. One side benefit of this awareness is that burrowing owls threatened by road, pipeline or other development are now reported to OBO or the Saskatchewan Environment and Resource Management so conflicts can be resolved without harm to the burrowing owls.

The OBO data set does provide the best data available on population trends of this species in Saskatchewan. The program now achieves a high level of reporting from its members, thus the value of the data for population monitoring will increase in the future. While the data contains an inherent bias because it begins with occupied sites, reoccupancy rates and new sign-ups provide a check on whether declines are real or due to that bias. One advantage of this method of population monitoring is that land-owner cooperation allows sampling of a substantial portion of the provincial population at a low cost.

The success of OBO has depended to a great extent on individual contact. The personal visit was remembered and has provided strong reinforcement of the importance of that site for nesting burrowing owls. Maintaining or increasing a level of personal contact will be essential to the continuing success of this program.

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ECOLOGICAL CONSIDERATIONS FOR MANAGEMENT OF BREEDING BURROWING OWLS IN THE COLUMBIA BASIN

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ABSTRACT.—Burrowing owl (*Speotyto cunicularia*) nest-site selection in the Columbia Basin appears to be based largely on the availability of potential nest burrows, vegetation structure, and food sources immediately adjacent to the burrow. Burrowing owls inhabiting the Columbia Basin of Oregon and Washington rely largely on badgers to excavate nest burrows (Green and Anthony 1989). However, badgers are also a major predator of burrowing owl nests (Green and Anthony 1989). To avoid badger predation by early detection, burrowing owls in the Columbia Basin tend to select burrows surrounded by either very short (≤5 cm) vegetation or a variety of elevated perches that provide good horizonal visibility around the nest site. They also appear to avoid nesting in shrub habitats where the average shrub coverage is >15%. In addition, burrowing owls often line their nest burrows with livestock dung, presumably to mask odors of nest occupants from potential mammalian predators. Burrowing owls also tend to select burrows surrounded by a high percentage ($\bar{x}$ = 55%) of bare ground, where prey (Heteromyid rodents and ground-dwelling arthropods) populations are presumably high.

Abandonment of nest sites tends to occur when distances between nest sites are less than 110 m, an important consideration when positioning artificial nest boxes. Furthermore, small nest boxes can become overcrowded by growing broods, often forcing movements of part of the brood to auxiliary burrows, potentially increasing the susceptibility of nestlings to predation or abandonment. Therefore, several aspects of burrowing owl nesting ecology, including predator avoidance, intraspecific competition, prey selection, and brood development, should be understood before designing a program for managing nesting habitat in a given area. In this paper we discuss nesting ecology and provide recommendations for managing populations of burrowing owls nesting in the Columbia Basin.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *management; Columbia Basin; Oregon; Washington; nest box; nesting.*

Consideraciones ecologicas para el manejo del tecolotito enano que se reproduce en Columbia Basin

RESUMEN.—La seleccion de sitios de anidamiento por el tecolotito enano (*Speotyto cunicularia*) en Columbia Basin parece estar basada en la disponibilidad de nidos madriguera, estructura de la vegetacion y fuentes de alimento adyacentes a la madriguera. Los tecolotitos enanos que habitan el Columbia Basin de Oregon y Washington dependen principalmente del tejon para que excave las madrigueras de anidar (Green y Anthony 1989). Sin embargo, el tejon es un principal depredador de nidos de tecolotito enano (Green y Anthony 1989). Para evitar depredacion por el tejon en base a pronta deteccion los tecolotitos enanos en Columbia Basin tienden a seleccionar madrigueras rodeadas por vegetacion corta (<5 cm) o una variedad de perchas elevadas que provean buena visibilidad horizontal alrededor del sitio del nido. Tambien parecen evitar anidar en habitats arbustivos donde la cobertura promedio de arbustos es > 15%. Ademas los tecolotitos enanos regularmente forran sus madrigueras con heces de ganado supuestamente para enmascarara los olores de los ocupantes del nido a los mamiferos depredadores. El tecolotito enano tiende a seleccionar madrigueras rodeadas por alto porcentaje ($\bar{x}$ = 55%) de suelo descubierto donde las poblaciones presa (roedores Heteromyide y arthropods de suelo) son presuntamente altas.

Abandono de nidos tiende a ocurrir cuando la distancia entre sitios de anidacion son menos de 110 m, una importante consideracion cuando se van a situar cajas artificiales de anidacion. Cajas chicas pueden sobrecargarse por las crecientes crias forzando movimientos de parte de la nidada a madrigueras auxiliares, potencialmente incrementando la susceptibilidad de los pollluelos a depredacion o abandono. Varios aspectos de la ecologia de anidacion del tecolotito enano incluyendo evitar depredadores,

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competencia intraespecifica, seleccion de presas, y el desarrollo de la nidada deben de comprenderse antes de diseñar un programa de manejo para habitat reproductivo en un area determinada. En este escrito discutimos ecologia reproductiva y damos recomendaciones para el manejo de poblaciones del tecolotito enano que anidan en Columbia Basin.

[Traducción de Filepe Chavez-Ramirez]

Management of wildlife habitat requires information on habitat selection and potential impacts to habitats important to the species of concern (Brown and Curtis 1985). Since Zarn (1974) suggested that burrowing owls (*Speotyto cunicularia*) require burrows surrounded by short, open vegetation, few authors (e.g., Craig 1974, Collins and Landry 1977, Andersen 1989, Haug and Oliphant 1990) have provided direct recommendations for managing burrowing owl habitat. Furthermore, no specific habitat management recommendations have been developed for burrowing owls breeding in the Columbia Basin region of Oregon and Washington. Finally, the unique ecology of this region (early rainfall patterns and lack of large, colonial sciurids), and this owl population's dependency on the badger (*Taxidea taxus*) for nest burrows (Green and Anthony 1989), suggest that management recommendations from elsewhere in the range (especially where owls depend on colonial sciurids for providing nest burrows) may not fully apply.

Herein, we describe several aspects of the nesting ecology of Columbia Basin burrowing owls, including predator avoidance, intraspecific competition, brood development, and prey selection, and present habitat management recommendations based on this information.

ECOLOGICAL CONSIDERATIONS

Several aspects of burrowing owl nesting ecology should be understood before designing a successful program for managing nesting habitat. Four of these aspects are the need to: (1) avoid predation; (2) avoid competition, especially with conspecifics; (3) meet the shelter demands of a large, growing brood; and (4) obtain an adequate food supply. The challenge in managing habitat for breeding burrowing owls is to recognize whether any of these needs are lacking and then to rectify, where possible, these inadequacies through manipulation or preservation techniques.

Predator Avoidance. A universal component of burrowing owl nest habitat is a burrow surrounded by short vegetation (Butts 1971, Coulombe 1971, Zarn 1974, MacCracken et al. 1985, Rich 1986, Green and Anthony 1989). Presumably, this lack of vegetation allows both adults and nestlings a commanding view of their surrounding environment and the ability to detect an approaching predator early enough to escape. Short vegetation is naturally found in prairie dog (*Cynomys* spp.) towns (Bonham and Lerwick 1976, Hansen and Gold 1977, Knowles et al. 1982) and this is probably why, besides burrow availability (Zarn 1974), prairie dog towns attract burrowing owls. Green and Anthony (1989) found that Columbia Basin burrowing owls nest successfully in grassland areas where the average vegetation height was <15 cm, but further found that when the average vegetation height was 5–15 cm, burrowing owls always selected a burrow with a nearby elevated perch. Green and Anthony concluded that the elevated perch allowed male burrowing owls to remain vigilant to approaching predators even after daytime soil surface temperatures became intolerably hot for standing on the ground. This is especially important if burrowing owls use their legs as heat dissipators as suggested by Coulombe (1971). Butts (1971) also noted that burrowing owls using badger burrows in Oklahoma nested within 90 m of a fence (i.e., a perch). Green and Anthony further concluded that an elevated perch was not necessary if the surrounding vegetation was short enough (≤5 cm) to allow the male a commanding view while peering over the lip of the burrow and keeping his legs in the burrow shade, a common surveillance posture at very short vegetation nest sites. Consequently, providing artificial perches may enhance burrowing owl nesting habitat in grassland areas where burrows and vegetation averaging <15 cm are present but natural perches are lacking. Our observations (unpubl. data) have shown that these perches can be as low as 20 cm, although when given several choices, burrowing owls preferred to perch at 1–2 m heights.

Habitats dominated by large, woody shrubs such as bitterbrush (*Purshia tridentata*) or big sagebrush (*Artemisia tridentata*) generally have an abundance of suitable perch sites (structurally stable shrubs). Green and Anthony (1989) suggested that one reason burrowing owls may have avoided rabbitbrush- (*Chrysothamnus* spp.) dominated habitats in their study area was because of the inability of these shrubs to support the weight of a perching owl. However, perch availability aside, Green and Anthony found owls to select shrub habitats where shrub volumes and coverage were considerably less than average, which may indicate a trade-off between maximizing view-enhancing perch numbers and minimizing the number of view-obstructing shrubs. In Green and Anthony's study 89% of the nest sites in shrub habitats occurred where shrub cover was <15%. We suggest using the 15% shrub cover value as a cut-off when selecting shrub habitats for managing for nesting burrowing owls.

Green and Anthony (1989) tested Martin's (1973) hypothesis that burrowing owls line their nest and tunnel entrance with cattle dung in order to avoid mammalian predators by masking nest odors. Of 15 nests lost to predation during one year of their study, only two (13%) were lined with dung. In contrast, of 32 nests which were successful, 23 (72%) were lined. Although their results do not fully conclude that cattle dung is a strong deterrent to mammalian predation, the evidence is compelling enough to warrant providing dung to nesting owls if not already available as a management consideration, especially if badgers occur in the area.

Intraspecific Competition. Burrowing owls nesting in large sciurid colonies are commonly found nesting in close proximity (<100 m) with apparently high nesting success (Butts 1971, Thomsen 1971). However, in the Columbia Basin, we found a high frequency of nest desertion when two pairs nested within 110 m (Green and Anthony 1989). We attributed this phenomena to competition by neighboring pairs over insect prey. This competition does not generally manifest itself until midway into the nesting cycle (late May to early July) when the owl's primary rodent prey, Great Basin pocket mice (*Perognathus parvus*) (Green et al. 1993), shift their activity underground in response to the Columbia Basin's very arid summer climate (O'Farrell et al. 1975). The disappearance of pocket mice forces nesting pairs to shift their forage attention almost exclusively to insects. Following the rules of Central Place Foraging Theory (Orians and Pearson 1979), owls must feed for small insect prey near the nest site where they eventually run into interference with nearby neighbors. Competition among pairs is not as evident early in the nesting season when rodent prey are abundant and pairs can forage at greater distances away from each other. This competition may also be exacerbated when available burrows greater than 110 m from existing nesting pairs is lacking.

Understanding this potential for high nest abandonment is important when using artificial nest boxes. We recommend that boxes be placed no closer than 110 m apart to help avoid competition stresses between neighboring pairs.

Brood Protection. The structure of artificial nest boxes may also affect nestling survival. While use of auxiliary burrows has been noted (Martin 1973, Henny and Blus 1981), we noticed this behavior was most apparent with owls using artificial nest boxes. We speculate that the standard artificial burrow configurations (30.5 × 30.5 cm; Collins and Landry 1977) we used can become too confining for large broods (i.e., >5) in advanced stages of development, forcing some nestlings to shift to auxiliary burrows. Broods in natural burrows expanded their nest chamber by digging the soft earthen walls. While we have no evidence that auxiliary burrow use decreases survivability of nestlings, we observed successful fledgings of more than seven members of a brood occurring only at natural burrows. We also observed that nestlings commonly widened the entrance to natural burrows allowing for several individuals to escape down the tunnel at once, whereas straight artificial tunnels generally only allow nestlings to escape single file. This could increase susceptibility to predation, especially by avian predators.

Based on our observations, we suggest that artificial nest boxes be constructed with walls at least 36 cm in length and width to accommodate large broods in advanced stages of development. Loose soil can be placed within the nest box along the sides to reduce the nest chamber size for attending females, but allow the nestlings easy means for expanding the chamber later. Three-wall designs would also allow nestlings to expand the nest chamber. Finally, a funnel design for the entrance may assist nestlings in quick escapes down the tunnel.

Prey Selection. An important component of the nesting habitat for Columbia Basin burrowing owls is a high percentage of bare ground. For example, Green and Anthony (1989) found that burrowing owls selected nest sites in areas where the average cover of bare ground was 55% and, conversely, the average cover of grass was only 28–36%, similar to findings ($\bar{x}$ = 35%) by MacCracken et al. (1985) for burrowing owls nesting in South Dakota. Dense grass may impede the movements (Tester and Marshall 1961, Rickard and Haverfield 1965, Gano and Rickard 1982) of important prey animals for local burrowing owls (Green et al. 1993). Also, higher populations of small mammals (Rogers and Hedlund 1980, Gano and Rickard 1982) and beetles (Rogers and Fitzner 1980) exist in shrub communities in the Columbia Basin with relatively low grass coverage. Vegetative and bare ground cover should be evaluated when selecting areas for establishing nesting pairs. Also, our observations of burrowing owls invading recently burned areas suggest that prescribed burning may be a useful tool for improving nesting habitat by removing dense grass cover.

Management Recommendations

With the rapid conversion of burrowing owl shrub-steppe nesting habitat to croplands in the Columbia Basin (Muckleston and Highsmith 1978), this species is becoming the focus of more management projects. Based on our earlier discussion, we provide a list of recommendations that consider several aspects of behavioral ecology including predator avoidance, intraspecific competition, brood protection, and prey selection. These recommendations are: (1) Provide elevated perches near potential nest burrows in grassland areas if the average vegetation height is 5–15 cm; (2) Provide fresh cattle dung near nesting areas if dung is not available and mammalian predators, especially badgers, occur in the area; (3) Place artificial nest boxes no closer together than 110 m; (4) Construct boxes with width and length dimensions of at least 36 cm and place soil around the inside wall; or construct boxes with only three walls. Make the tunnel entrance funnel-shaped; (5) Select sites for establishing or increasing nest sites that have approximately 55% (40–70%) bare ground and average shrub coverage of <15%; and (6) Conduct research on the utility of prescribed burning as a tool for enhancing owl nesting habitat.

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THE ONE-WAY DOOR TRAP: AN ALTERNATIVE TRAPPING TECHNIQUE FOR BURROWING OWLS

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ABSTRACT.—A population of 17 burrowing owls (*Speotyto cunicularia*) had to be removed from a construction site in Manteca, San Joaquin County, CA, in a two-week period. I used a trapping method that incorporated a one-way door surrounded by a wire mesh cage. One-way doors and cages were placed over burrow entrances so that owls were able to exit burrows yet remain within the cage (trap). Initial attempts using snare-type traps captured eight owls, yet proved to be time-consuming. The remaining nine owls were captured in half the time it took to capture the first eight owls. The ease of constructing and setting the trap, the potentially high capture rate, and the lack of trapping injuries, makes the one-way door trap an efficient alternative to other capture techniques.

KEY WORDS: *burrowing owl;* Speotyto cunicularia; *technique; trapping.*

La puerta de una sola direccion: Una tecnica alternativa para atrapar tecolotito enano

RESUMEN.—Una poblacion de 17 tecolotitos enanos (*Speotyto cunicularia*) se tuvieron que remover de un sitio de construccion en Manteca, condado San Joaquin, California, durante un periodo de 2 semanas. Use un metodo de atrapar que incorpora una puerta de una sola direccion rodeada de malla de alambre. Puertas de una sola direccion y jaulas se pusieron sobre las entradas de las madrigueras para que los tecolotes pudieran salir pero quedaban atrapados en la jaula. Atentados iniciales usando el metodo de trampas de lazo atraparon ocho tecolotes pero era demasiado tardado. Los otros nueve tecolotes se capturaron en la mitad del tiempo que se requirio para atrapar los primeros ocho tecolotes. La facilidad con la que se puede construir y plantear la tramp, la alta probabilidad de captura y el evitar lastimaduras hacen que la trampa de puerta de una sola direccion sea una alternativa eficaz a otras tecnicas de captura.

[Traducción de Filepe Chavez-Ramirez]

Methods for capturing burrowing owls (*Speotyto cunicularia*) include bal-chatri traps (Berger and Mueller 1959, Ward and Martin 1968, Smith and Walsh 1981, Yosef and Lohrer 1992), noose carpets (Bloom 1987), noose rods (Winchell and Turman 1992), mist nets (Ferguson and Jorgensen 1981), padded leg-hold traps (Haug and Oliphant 1990), and variations of Havahart or Tomahawk-type traps (Martin 1971, Ferguson and Jorgensen 1981, Plumpton and Lutz 1992). However, these traps can be time-consuming, labor intensive, and capable of capturing only one or two owls at a time. The objective of this study was to capture and relocate 17 burrowing owls, during the fledgling stage, from a construction site in Manteca, California, within a two-week period during summer 1992. Initial attempts to capture owls using one bal-chatri trap baited with a mouse and three noose carpet traps per burrow were successful, yet time-consuming. In addition, owls became trap-shy and eventually avoided the snare traps. For this reason, I developed and utilized a trapping technique incorporating a one-way door and cage to increase the capture rate.

MATERIALS AND METHODS

One-way doors were placed in the entrances of occupied burrows during mid-day after owls had descended into burrows to avoid high ambient temperatures. Each burrow entrance was then enclosed with a square 61cm × 61cm open-bottomed cage (Fig. 1). The one-way doors were constructed from 10.2 cm aluminum heating duct secured to a 10.2 cm metal collar. A clear, lightweight, Plexiglas door was attached to the ceiling collar with duct tape. The one-way door is designed to allow an owl to exit a burrow, but not reenter. Minor modifications were sometimes required for the installation of the one-way door. A cage was placed over each one-way door to capture exiting owls. The cage was anchored to the ground by tent stakes or bricks. Cages were constructed with poultry mesh and 2.54 cm PVC pipe. A trap door was cut into the top of the cage to permit removal of captured owls. Trapping occurred July 1992, between dusk and 0100 h and during early morning hours (i.e., 0500 to

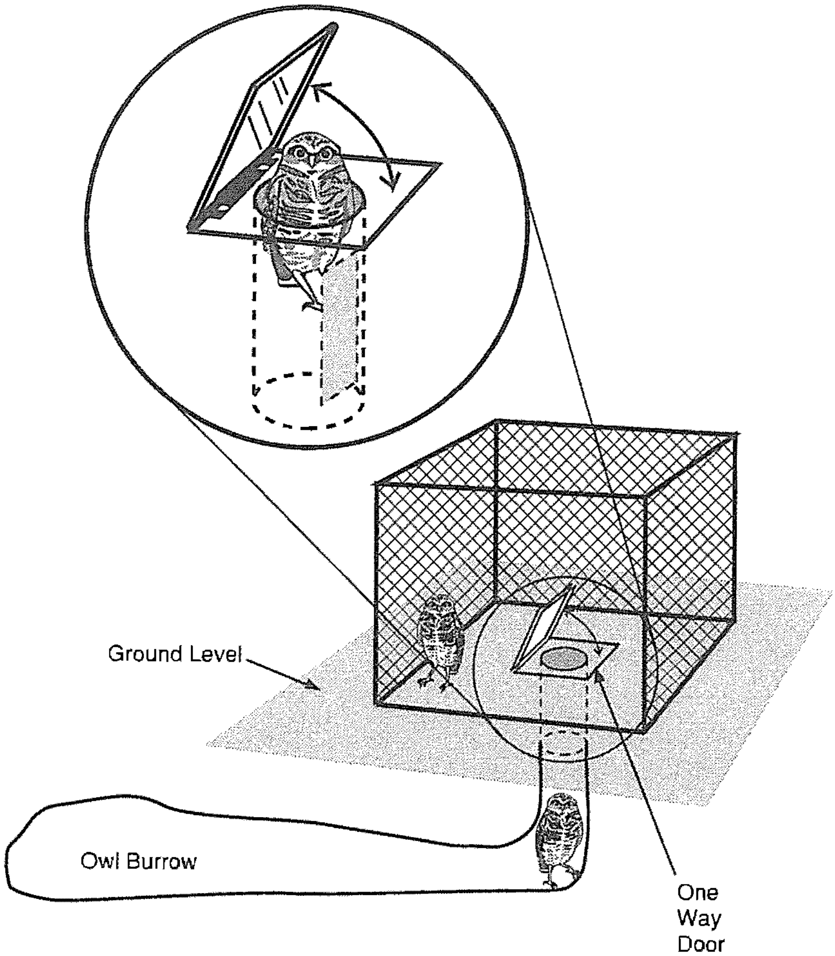

Figure 1. A one-way door trap for burrowing owls.

0900). Traps were monitored on an hourly basis. Captured owls were immediately removed and banded with U.S. Fish and Wildlife Service aluminum bands and plastic color leg bands.

RESULTS AND DISCUSSION

Eight owls (six juveniles and two adults) were captured in 35 person-hours with an average of one bal-chatri and three noose carpet traps per burrow. This effort resulted in one owl capture per 4.3 hr, yet only half of the population had been captured. In contrast, the remaining nine owls (four adults and five juveniles) were captured in 19 person-hours using 4 one-way door traps (one trap per burrow). Six of the nine owls were captured in less than 2.5 hr, four of which were caught within a 15 min. time span, in three traps. Twice, two owls were captured in a single trap. Overall, the one-way door trapping effort resulted in one owl capture per 2.1 hours.

The one-way door trap captured nine owls twice as fast as the bal-chatri and noose carpet attempts. The one-way door trap captured adults and juveniles, whereas bal-chatri and noose carpets resulted in a predominance of juveniles. Multiple captures occurred twice, indicating a potential for capturing entire families in one attempt. All captured owls were unharmed and appeared calm while in the traps. Potential owl injuries can be further avoided by using an alternative material for the cage construction (e.g., plastic or nylon).

The ease of constructing and setting the trap, the minimal disturbance to the burrow, the lack of trap injuries and escapes, and the potentially quick rate of capture makes the one-way door trap an efficient alternative to mist nets, snare-type traps, padded leg-hold traps, and box traps.

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AGE IDENTIFICATION OF NESTLING BURROWING OWLS

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ABSTRACT.—Two rescued burrowing owl (*Speotyto cunicularia*) nestlings hatched and raised for release in a rehabilitation program were photographed during their first month of growth. The owls were weighed regularly and notes were taken of plumage changes and behavior. They were self-feeding and tearing up halved dead mice by 15 d.

KEY WORDS: *burrowing owl*; Speotyto cunicularia; *weights*; *nestling plumage*; *feeding ability*.

Identificacion de polluelos del tecolotito enano

RESUMEN.—Dos pollos rescatados de tecolotito enano (*Speotyto cunicularia*) que se empollaron y criaron para liberarlos en un programa de rehabilitacion se fotografiaron durante el primer mes de crecimiento. Los tecolotitos se pesaron regularmente y se tomaron apuntes de cambios en el plumaje y conducta. Los tecolotitos comian solos y destazaban ratones medio muertos a los 15 dias.

[Traducción de Filepe Chavez-Ramirez]

Burrowing owls (*Speotyto cunicularia*) in Santa Clara County, California were being routinely buried at construction sites. Nestling owls had little or no protection from earth-moving equipment, unless they were accidentally discovered. As director of a wildlife rehabilitation department for a local humane society in 1982, I started a burrowing owl rescue, relocation, and education program until better methods of burrowing owl preservation could be implemented. With the permission of the California State Department of Fish and Game and the U.S. Fish and Wildlife Law Enforcement officers, a team of volunteers and I removed only nests of owls that would otherwise be destroyed by construction equipment. This sometimes involved removal of eggs. After several years of raising nestlings and some hatchlings at our facility, we started receiving calls for advice on burrowing owl care from other rehabilitators in California. We found it difficult to estimate age and condition of the owlets over the telephone. Our initial literature searches had not indicated any useful information on the development of this species. Therefore, it became necessary to establish some comprehensive guidelines for aging burrowing owl young. My objective was not to compare weights and growth, but to have a general guideline of aging by plumage and weight. The following information is based on only two subjects and is intended as only a guideline. It is not a rigorous scientific study.

METHODS

In 1986 we removed three burrowing owl eggs from an active construction site in Santa Clara County, California. They were hatched on 3–5 June at the Predatory Bird Research facility in Santa Cruz, California. After the chicks were returned for raising, I selected the first and last birds hatched from the clutch to photograph and weigh. The three siblings were kept together. The nestlings were color-banded for identification and photographed at two d intervals or longer during the first month of growth. A box was laid on its side on a desk with a ruler propped upright inside. A Pentax K-1000 camera with a 50-mm lens was set on a tripod at approximately 1 m from the desk. Each two or three d the two owlets were removed from the nest area prior to their first morning feeding, placed next to the ruler, and photographed. With the exception of one 7-d period, the owls were weighed on a triple beam balance scale. I noted behavorial changes and development. The nest area was initially a large darkened tub with a K-101 K-pad at one end for an optional heat source. This pad is warmed by circulating warm water which produces a non-drying heat for brooding. The owls were fed commercially and home-raised dead mice, crickets, mealworms and beetles. Their food was not weighed. They were graduated to a large carrier with a burrow-type nest box and then at 30–32 d to a 3.05 m × 6.10 m flight aviary, complete with in-ground burrows. I worked alone and quietly when handling the owls. I sometimes mimiced their vocalization, which was a raspy "pssssst, pssssst." Because these owls were in rehabilitation and for release there was as little human contact as possible. It became increasingly difficult to persuade them to stand in position in the photo area and photography was impossible after 30–32 d of age.

Table 1. Plumage changes of two nestling burrowing owls observed in captivity.

DAYS OF AGE	PLUMAGE CHARACTERISTICS
8	Wings, head, back and nape pinned. Head is darkening with pin feathers. Second down blooming* on tibiotarsus and breast.
11	Back feathers emerging.
13	Primaries pinned 20 mm, back feathers emerging at nape and shoulders, upper breast covered with second down, tarsus pinned. Throat pinned. First down visible and sparse.
15	Body covered with second down. Legs feathering. Head feathering. First down still visible on head. Second down on wing coverts.
17	Primaries blooming and visible, back feathering well, some throat feathering with dark brown edge.
19	Primaries blooming and visible, back feathering well, some throat feathering with dark brown edge.
22	Throat is white with dark edge.
24	Tail pinned 12.5 mm.
26	Legs well feathered, small trace of white down on crown.
28	Little change.
30	Tail emerging.
32	Juvenile breast feathers emerging, tail 25 mm long. First down barely visible.

*The term "blooming" is used to describe the opening of the feather from the shaft.

Figure 1. Burrowing owls at selective ages. A, Eight days. B, Eleven days. C, Fifteen days. D, Twenty-one days. E, Thirty-two days.

RESULTS AND DISCUSSION

The burrowing owls went through two down plumage stages. The first down, at hatch, was white; the second down, which emerged at about 8 d of age (on the breast, flank, and wing covert area) was tan. (Table 1 and Figure 1). I did not record observations on these two owls prior to eight d of age. I do, however, have notes and weights on earlier ages from more recently-hatched burrowing owls which are not included it this paper. The older owl weighed more than the younger owl when photographed at the same age (Table 2). Weights might be affected during the self-feeding period. The primary purpose of these owls was rehabilitation, so regular routines were upset as little as possible. I did not determine light availability during the photographing period; however, hand-raised birds are allowed normal daylight hours in a non-heated room, with open windows until they are

Table 2. Weights of two captive-raised burrowing owl nestlings. Owl A was hatched 3 June 1986 at 0500 H; Owl B on 5 June 1986 at 2315 H.

DATE	BIRD	WEIGHT (g)	DAYS OF AGE
13 June	A	63.0	10
	B	45.5	8
16 June	A	123.0	13
	B	81.5	11
18 June	A	122.0	15
	B	97.0	13
20 June	B	108.0	15
24 June	A	142.0	21
	B	125.0	19
27 June	A	161.0	24
	B	140.0	22
5 July	A	177.0	32
	B	143.0	30
9 July	A	151.0	36
	B	143.0	34

transferred into an outside flight aviary. I noted that on d 11 mouse pieces were being picked up (Table 3). I did not distinguish in my notes which of the owls had consumed the mouse bits. It has been my practice to feed nestling burrowing owls from below, rather than from above, and drop mouse bits or insects in front of them in order to draw their attention to the food, not the feeder, and to encourage self-feeding. I have observed younger burrowing owls (prior to eyes opening) walking about the nest tub on their ankles at feeding time with their faces to the floor, turning their heads from side to side in a sweeping motion, calling and biting at anything.

Table 3. Behavior and development of captive burrowing owls (based on general notes taken of three nestling owls).

DAYS OF AGE	BEHAVIOR AND DEVELOPMENT
8	Walks and sits on ankles, can stand.
11	Eyes opening, can stand, will pick up mouse bits from floor of nest area.
13	Eyes open, standing well, some defensive posturing.
15	Self-feeding, tearing up halved mice.
17	Doing defensive posturing in my presence.
19	Independent aud self-feeding.
21	Tearing up whole mice.
26	Alert, independent, objects to handling.
32	Uncooperative, wants no part of humans.

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OBSERVATIONS, RESIGHTINGS, AND ENCOUNTERS OF REHABILITATED, ORPHANED, AND RELOCATED BURROWING OWLS

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Abstract.—This paper describes data on 46 burrowing owls (*Speotyto cunicularia*), of which 40 were part of an ongoing rehabilitation and release program at the University of California, Davis, (UCD) and the others the subject of two unrelated relocation efforts between 1981 and 1991. Of the 40 owls which came to the UCD Raptor Center as the result of illness, injury, or being orphaned, 9 died or were euthanized; 9 were non-releasable and transferred to other institutions for breeding and/or research; 6 were released unbanded; and 16 were banded and released in occupied or unoccupied burrows within an established colony on the UCD campus. Nine orphaned HY owls were fostered, five of which (55%) were encountered or resighted. Two were encountered 3 and 5 days postrelease after colliding with large windows near the release site. One owl encountered 12 d postrelease was retrapped at the release site. Two other fostered owls were resighted up to 28 days and 34 d postrelease, respectively. These two used both the original release burrow and satellite burrows within 27 meters. Of 5 adult rehabilitated owls released, one was found 80 d postrelease after colliding with a vehicle (CV) approximately 183 m from the release site. Two adult owls were trapped and then relocated 0.8 km on the campus of the University of California, Davis, in December 1981; they were encountered 426 d (dead due to CV) and 1,310 d (retrapped near the release site) respectively. In a separate relocation project using one-way burrow exits on the Consumnes River College campus, all owls relocated themselves to artificial burrows placed 45 m away between November 1988 and January 1989. In another effort, in June 1991, six burrowing owls were relocated from a development site in Sacramento; three owls relocated 24 km from the site and three relocated 48.3 km. Of the 6 relocated owls, 5 were observed between 10 and 49 d postrelease. One adult female observed 10 d at the relocation site returned 24 km to her original territory, arriving 32 d postrelease. These data suggest that although some burrowing owls develop a strong fidelity to a relocation site, others tend to disperse after a period of adjustment at the site of release.

Key Words: *burrowing owl;* Speotyto cunnicularia; *relocation; rehabilitation; fostering; resighting; encounter; mortality; California.*

Observaciones, reobservaciones, y encuentros de tecolotitos enanos rehabilitados, huérfanos, y relocalizados

Resumen.—Este escrito describe datos sobre 46 tecolotitos enanos (*Speotyto cunicularia*) de los cuales 40 fueron parte de un programa de rehabilitacion y liberacion de la University of California, Davis, (UCD). Los otros eran parte de dos esfuerzos no relacionados de relocalización entre 1981 y 1991. De los 40 tecolotes que llegaron a UCD Raptor Center como resultado de enfermedad, lastimadura, or por ser huérfanos, 9 murieron; 9 no se podian liberar y se transfirieron a otras instituciones para su reproduccion y/o para investigacion; 6 se liberaron sin anillar; y 16 se anillaron y se liberaron en madrigueras ocupadas o no ocupadas en colonias en el campus de UCD. Nueve tecolotitos huerfanos del año se criaron, de los cuales cinco se encontraron o se reobservaron Dos se encontraron 3 y 5 días después de haberse liberado cuando chocaron con grandes ventanas cerca del sitio de liberacion Un tecolote encontrado 12 días después de liberarse se atrapo en el sitio de liberacion. Otros dos tecolotitos criados se reobservaron hasta 28 y 34 días después de liberarse. Estos dos utilizaron la madriguera de liberacion y madrigueras satélites hasta 27 metros. De 5 tecolotes adultos rehabilitados y liberados, uno se encontro 80 días después de liberarse cuando choco con un vehículo (cv) aproximadamente a 183 metros del sitio de liberacion. Dos tecolotes adultos se atraparon y se relocalizaron 08 km en el campus de la

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University of California, Davis, en diciembre 1981; se encontraron 426 dilas después (muertos debido a cv)y 1,310 días (reatrapado cerca del sitio de liberacion), respectivamente. En un poyecto diferente de relocalizacion utilizando salidas de-una-sola-direccion en el campus de Consumnes River College, todos los tecolotes se relocalizarón independientemente a madrigueras artificiales puestas a 45 metros entre noviembre 1988 y enero 1989. En otro esfuerzo, en junio 1991, seis tecolotitos enanos se relocalizaron de un sitio en desarrollo en Sacramento; 3 tecolotes se relocalizarín 24 km del sitio y tres se relocalizarón 483 km. De los 6 tecolotes relocalizados 5 se observaron entre 10 y 49 días después de liberarse. Un hembra adulto observada 10 días en el sitio de relocalización regreso 24 km a su territorio original arribando 32 días después de liberarse. Estos datos sugieren que aunque algunos tecolotitos enanos desarrollan gran fidelidad a su sitio de relocalización, otros tienden a dispersarse después de un periodo de ajuste en el sitio de liberacion.

[Traducción de Felipe Chavez-Ramirez]

Burrowing owls (*Speotyto cunicularia*) were rehabilitated and released within an established colony on the University of California, Davis (UCD) campus in order to augment a declining population and to observe and document postrelease behavior, survival, and mortality (Johnson and Schulz 1985). The burrowing owls on the UCD campus provided a valuable resource for both undergraduate and graduate studies and allowed the public an opportunity to view and further appreciate this unique and relatively visible owl. To mitigate the effects of the campus maintenance and development, the UCD Raptor Center, School of Veterinary Medicine, worked closely with the campus grounds division to manage the available nesting and foraging habitat on behalf of the burrowing owls. Occupied burrows were located and identified. Burrows were considered occupied if they had adult owls using them and/or they had fresh pellets, fecal droppings, and feathers at or near their entrance. Soil in the PVC pipe brought in by the owls' feet was another indication of activity in the burrow. The grass was periodically mowed to a height of approximately 15.2–22.9 mm, artificial perches were erected, and six artificial burrows were constructed and placed in one of the burrowing owl habitats (Collins and Landry 1977) and (Olenick 1987). The UCD Raptor Center staff also worked closely with rodent control personnel and participated in annual control meetings by giving talks on how to identify occupied burrows to assure that owls were not indiscriminately poisoned or gassed and that rodent control did not take place in fields inhabited by burrowing owls. In addition, UCD Raptor Center staff, local conservation groups, and concerned citizens convinced campus officials to set aside the nesting areas and place informative signs and fences on the periphery of burrowing owl habitat. A committee was formed to advise the campus on natural resources and open spaces. Despite these efforts, the burrowing owl disappeared from its former nesting areas on the UCD campus by 1991 (Johnson 1992). This paper provides information on the fates of 22 burrowing owls released between 1981 and 1991.

STUDY AREA AND METHODS

The UCD campus is located in the Sacramento valley 24 km west of Sacramento in Yolo County, California. The burrowing owl habitat was in flat, open, ruderal fields that had populations of the California ground squirrel (*Spermophilus beecheyi*). Injured and orphaned owls were initially treated at the UCD Veterinary Medical Teaching Hospital when necessary and then transferred to the UCD Raptor Center (California Raptor Center) for observation and rehabilitation. Hatching year (HY) birds without injuries were evaluated and released (fostered) on campus as soon as possible into burrows occupied by wild pairs with young of similar ages (Olendorff et al. 1980).

Adult injured owls were initially rehabilitated using physical therapy and then placed in flight cages until they were capable of strong, even flight ability (Schulz and Horowitz 1982; Horowitz, Schulz, and Fowler 1983). Sixteen out of 22 rehabilitated owls released were banded with U.S. Fish and Wildlife Service bands. Release areas were monitored using 7 × 42 binoculars at least four mornings a week until the released birds could no longer be located.

Three relocation projects are of special interest. The first occurred in 1981 when two adult birds were trapped with monofilament noose (bal chatri) traps at burrow entrances and relocated approximately 0.8 km from one area of the campus to another.

Another relocation project at Consumnes River College in southern Sacramento County was undertaken in 1989. The purpose of the relocation was to prevent accidental destruction of burrowing owls living in burrows on the site of an impending new road coustruction project. Six artificial burrows were placed 45.7 m south of the construction area on a north and west facing berm that surrounded a football field. The burrows were constructed with 152.4 mm diameter corrugated PVC pipe extending 120 cm into the side of the berm and turning 90° for another 120 cm into a 34.8 cm by 47.4 cm rectangular nest chamber constructed of cement. The base of the chamber was open and had 30 cm of rock and sand base for drainage. The area was surveyed on six different days between 6 November 1988 and 21 January 1989. In January 1989, five, one-way exits (Johnson 1992) were placed in the entrance to active burrows at the construction site. The one-way exits remained in place for one week to prevent reentry into burrows by the owls. At the end of the week burrows were filled with dirt. This method has the advantage of not requiring trapping or hands-on manipulation of the owls.

In a third project in 1991, six burrowing owls were trapped with noose traps and relocated to mitigate for future development in their habitat. Their habitat (in ruderal fields) was in a populated urban area of Sacramento, California. Three of the birds were relocated at artificial burrows on the UCD campus 24 km west of the original site, and the other three were relocated approximately 48.3 km west of the original site to a nonnative grass field with artificial burrows approximately 9.6 km north of Winters, Solano County, California. One dead mouse per bird and approximately 200 live crickets were placed in each burrow entrance. Monitoring alternated each day at sunrise and sunset, respectively.

Results and Discussion

A total of 40 sick, injured, or orphaned burrowing owls were treated by the UCD Raptor Center between 1980 and 1988. Twenty-two (55%) were eventually released. Of the 17 HY burrowing owls, 43% were received in June and 19% in July. Six (28%) of the 23 adult burrowing owls were received between June and September. Burrowing owls were brought to the UCD Raptor Center for a variety of reasons, the most noteworthy (25%) being collisions with vehicles (CV). Four owls (9%) collided with large windows or buildings. Fourteen (32%) had either wing fractures or coracoid fractures; 4 of these (29%) were eventually released. Nine (22.5%) owls died or were euthanized, and 9 were nonreleasable and transferred to other institutions for breeding and research projects.

Five of the nine HY owls fostered into occupied nests were encountered or resighted. Two of these were encountered three and five days postrelease, respectively, due to collisions with large windows; one was encountered 12 days postrelease and was retrapped (Johnson pers. comm.) at the release site; and the remaining two were resighted up to 28 and 34 days, respectively. Fostered owls appeared to interact normally with nonsibling juveniles and were fed by adults. They used satellite burrows within 27 m of the release site burrow. The method of fostering HY owls into active burrows with similar age birds allowed the young, inexperienced owls time to socialize with nonsibling conspecifics and sharpen their prey-catching skills while being fed by adult owls (Olendorff et al. 1980). However, more data are needed to evaluate the success of this technique. It is not known what caused the owls to fly into windows, although stray dogs were frequently seen chasing owls in the fields on campus. Dogs have also been observed chasing ground squirrels and digging at burrow entrances. Cats in the owl habitat could also have had a serious impact on the population.

Only one adult of seven injured and rehabilitated adult owls was later encountered. This individual had a coracoid fracture on 29 October 1985 and released 17 January 1986 on the UCD campus. It was encountered approximately 183 m from the release site after 80 d, dead due to CV.

The two adult owls trapped on the UCD campus in December 1981 were relocated 0.8 km to another site on campus. The first encounter was 28 November 1983, 426 d postrelease. The owl was dead due to CV approximately 0.8 km from the relocation site. The second relocated owl was retrapped near the release site in good condition on 6 June 1985, 1,310 d postrelease (Johnson pers. comm.).

From 1980 to 1990, 22 burrowing owl deaths were documented on the UCD campus. Ten of these (45%) were CVs; five (22.7%) were killed by feral (domestic) cats; four (18%) collided with windows; and three (13.6%) died of unknown causes. Therefore, 20 owls were documented to have been hit by vehicles (half survived as noted earlier). Their low, undulating flight behavior may be an important factor in their susceptibility to collisions with moving vehicles.

In the passive relocation effort at Consumnes River College, all six owls relocated themselves, and at least two were observed at the entrance to the artificial burrows within 1 wk. More owls were observed on the stadium berm during subsequent surveys. No owls were seen at the construction site after their burrows were destroyed. Although owls moved from the construction area into artificial burrows 45.7 m away, there is no certainty that the individuals observed were the same birds because they were not banded. However, Trulio (pers. comm.) observed that by using the technique described above, banded owls successfully relocated themselves into nearby artificial burrows.

In the third relocation effort involving six burrowing owls, the three owls relocated from Sacramento to the Davis campus were a mated pair with one juvenile approximately 6–7 wk old. The female remained at the release site up to 10 d and was later observed at her original territory after 32 d. She was retrapped and relocated but did not remain more than a day. The juvenile was observed for at least 14 d and was not seen after that. The adult male was observed 49 d postrelease near the relocation site. The other three nonmated owls relocated approximately 48.3 km west of the original site and 9.6 km north of Winters, California, were placed into separate artificial burrows. Two of the owls were resighted at the relocation burrows up to 24 and 42 d, respectively. The third owl was not observed after release.

These data suggest that some relocated owls may remain at release sites while others tend to disperse and even return to their original territory after a period of adjustment. Although relocation efforts may temporarily remove individual owls from potential destruction, more data are needed on long-term effectiveness. This method of mitigation should be carefully considered and only used as a last resort.

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BURROWING OWL SITE TENACITY ASSOCIATED WITH RELOCATION EFFORTS

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ABSTRACT.—A pair of burrowing owls (*Speotyto cunicularia*) exhibited strong site tenacity during an effort to relocate them from a development site in San Joaquin County, California during the winter and fall of 1992. This case prompted an inquiry among other biologists working with burrowing owls to see if they had had similar experiences. Their responses allowed me to present additional examples of site tenacity in efforts to relocate burrowing owls along the Pacific coast. Potential benefits of site tenacity and considerations for relocation success are also discussed.

KEY WORDS: Speotyto cunicularia; *burrowing owl; California; relocation; Washington; British Columbia.*

Tenacidad de sitio asociada con esfuerzos de relocalizacion de tecolotitios enanos.

RESUMEN.—Un par de tecolotitos enanos (*Speotyto cunicularia*) exhibieron fuerte tenacidad de sitio durante esfuerzos para relocalizarlos de un sitio en desarrollo en el condado San Joaquin, California durante invierno y otoño de 1992. Este caso causo que averiguara entre otros biologos trabajando con el tecolotito enano para determinar si habian tenido experiencias similares. Sus respuestas me ayudaron a presentar ejemplos adicionales de tenacidad de sitios observados en esfuerzos de relocalizacion de tecolotito enano a lo largo de la costa del Pacifico. Beneficios potenciales de tenacidad de sitio y consideraciones para el exito en relocalizacion tambien se discuten.

[Traducción de Filepe Chavez-Ramirez]

There are at least three reasons to relocate burrowing owls: to (1) protect them from risk when their habitat is being altered or destroyed; (2) rebuild depleted burrowing owl populations by translocation from healthy populations; and (3) protect endangered prey species.

Two relocation methods have been used with considerable variation of technique in removing burrowing owls from a particular location. The first is removing the burrow systems by digging out or closing burrows, leaving the owls to independently relocate. This method is usually applied when it has been found that there is nearby or adjacent habitat available. The second is trapping and relocating the owls directly to a new site which is considered to be suitable habitat some distance from the original site.

Along the Pacific states, particularly in the San Francisco Bay area, there have been a number of projects involved with moving burrowing owls, resulting in varying degrees of success (Dyer 1991, Harris and Feeney 1989, H.T. Harvey & Assoc. 1993). Occasionally, burrowing owls can show considerable original site tenacity causing complications and negative results. Burrowing owls at a development site in San Joaquin County, CA led me to investigate the topic of site tenacity and compile information from several sources. Source material for additional information came from biologists and consulting firms willing to share their experiences. Although information from some of the cases is anecdotal, and some specific details have been lost in time, the fundamental lessons learned can assist those who find it necessary to move and/or protect burrowing owls.

In December of 1991, I was asked to move a pair of burrowing owls from a cul-de-sac of lots with partial improvements already installed so that the builder could finish constructing homes during the spring of 1992. The site is in the city of Tracy in San Joaquin Valley, California. Several open fields were available to these owls within a few hundred meters of their burrow. Some of these held owls, and most had ground squirrels and unoccupied burrows. After consulting with the California Department of Fish and Game, it was decided to close out the burrows of the resident owls on the construction site, and let the owls relocate themselves. Evening observations showed that the owls were compatible with and foraged with four pairs of owls nearby.

METHODS

The first burrow closure effort was initiated in January, 1992 by flushing the birds on several occasions to confirm that they were familiar with available nearby unoccupied burrows. The owls flew directly to burrows either in the adjacent field or to burrows along a drainage canal within 100 m. The owls' main burrow and satellite burrows on the development site were then dug out and filled in. Burrows were closed until it was confirmed that the burrowing owls had chosen a home burrow off the site. I made twenty-nine visits (involving about 90 hr) to the site between 21 Jan. 1992–22 Mar. 1992. One visit was made to the site in April, 1992 and then twice a month through May, June, July, and August 1992 to monitor the activity and location of burrowing owls on the site and in adjacent fields during the breeding season. In addition, local homeowners and a schoolteacher, who wanted to protect the owls, monitored the owls almost daily.

The second burrow closure effort at the same site began in early September 1992 and continued until late November 1992. The second effort received continued support from local citizens. Four artificial burrow systems were constructed beginning at 100 meters from the cul-de-sac site on the bank of the drainage canal, each system separated by 35 m. The burrow cavities were made of heavy plastic water valve boxes (25.4-cm × 40.6-cm at the top; 30.5-cm deep) with removable lids. Two holes were cut in the end for the placement of four-inch plastic corrugated tubing, and a portion of one side of the box was removed so the burrow cavity would have at least one dirt wall. The boxes were buried <1m underground. Light-colored sand was placed at the entrance of the burrows to facilitate easy reading of tracks into the burrows. Burrowing owls from the cul-de-sac site were flushed from the site beginning 18 Sept. 1992. Burrows at the cul-de-sac were filled in after flushing the birds from the site. Closing burrows and flushing the birds continued until the owls were no longer observed at the cul-de-sac development site. Thirty visits (84 hr) were made to the site from 3 Sept. 1992–29 Nov. 1992.

RESULTS

The first effort (January–March 1992) to remove the burrowing owls from the cul-de-sac site resulted in having to close burrows thirteen times at the cul-de-sac before the owls chose another burrow on the berm of the nearby canal, 100 meters away. They stayed off the cul-de-sac site for at least two weeks in March. In late April 1992, it was reported that one of the pair which had moved to the canal had been shot with a pellet gun (Linda Smith pers. comm.) and presumably its mate returned to the cul-de-sac where ground squirrels (*Spermophilus beecheyi*) reopened some of the closed burrows. At about the same time, four additional owls (two pairs) moved to the cul-de-sac area. There were then five burrowing owls residing on the development site, and it was their breeding season. The property owners agreed to let the birds use the property for the 1992 breeding season, but requested that we renew efforts to remove them from the site in September of 1992. Visits through the summer revealed that the two pairs of owls had young, and that a single bird remained on the site, always seen alone at the same burrow. On 3 Sept. 1992 the two burrowing owl families were absent from the development site; however, the single bird was present at its burrow on the cul-de-sac. On 6 Sept. 1992 the burrow occupied by the single bird hosted two adult birds, suggesting that the single bird had acquired a mate. The birds were, however, unbanded, so this late summer pairing could not be confirmed.

Flushing the birds from the site and filling in burrows began again on 18 Sept. 1992 after owl tracks had been seen at all of the new artificial burrow entrances. Most observations in late September and October revealed a pair of owls at burrows on the cul-de-sac which were either opened by ground squirrels or the owls themselves. One owl was observed digging on two occasions at locations where burrows had been filled. I closed any burrows I found opened by animals on every visit. On two visits the owls were found huddled under vegetation near their closed burrow with no other burrows available. A shooting incident on the cul-de-sac resulted in the killing of two rock doves (*Columba livia*) with a pellet gun, and possibly caused the injured right leg on one of the owls observed at the same time (13 Oct. 1992). The incident appeared not to deter the owls; they remained at the cul-de-sac. A burrow was opened for the injured bird which the pair used; however, trapping efforts to catch and rehabilitate the injured bird failed. The burrow was closed again on 21 Oct. 1992. The birds were last seen at the cul-de-sac on 6 Nov. 1992, and missing on 8 Nov. 1992. Neither the injured bird nor any additional birds could be located at nearby fields or other local habitat during subsequent visits through November 1992.

Two pairs of burrowing owls successfully fledged young at the canal where artificial burrows were placed during both the 1993 and 1994 breeding season (Larry Vasco pers. comm.) indicating that the artificial habitat attracted some of the local burrowing owls even though the target owls initially resisted moving to the area.

Other Case Histories

The site tenacity exhibited by burrowing owls in San Joaquin County led me to inquire among colleagues to see if they had had similar results with burrow closure or relocation efforts. In addition to a second experience I had (Case 2, below), I received three accounts of birds remaining at sites after burrow closure, nine accounts of banded owls that returned to original sites after relocation, and one relocation effort (Case 8) that resulted in no return. Details of each case varied considerably, with relocation distances from 1–150 miles and original sites located from San Diego, California to central Washington. Another factor that varied considerably was the time of year. Relocation efforts from January through December had at least some burrowing owls resisting a new location by staying at or returning to the original burrow sites. Brief accounts of these cases follow.

Burrow Closure

Case 1. Lake Elizabeth, Fremont, Alameda Co., CA.

Reason	No. Owls	Season	Nearest Habitat
Vandalism	2	Breeding	Adjacent

Vandals destroyed eggs in a shallow nest and blocked burrow entrance. Burrow was closed for about a week. Owls were not banded and were not detected when burrow was opened, but one week after burrow was opened a pair of owls was found at the burrow. Only one pair was known in the vicinity, and the owls at reopened burrow were presumed to be the same that lost their nest.

Case 2. Alameda, Alameda Co., CA.

Reason	No. Owls	Season	Nearest Habitat
Development	2	Fall/Winter	Adjacent

In November 1986 the location of a burrow used by a pair of unbanded owls was leveled, graded and completely cleared of vegetation. A pair of owls, presumed to be the same birds that lost their burrow, was seen on several occasions near the destroyed burrow site. They were last seen on 5 Jan. 1987 using a pile of discarded construction materials about 100 m from the burrow site for cover. The following day a 10-ft-wide ditch was created at the location of the debris pile; the owls could not be found.

Case 3. Cedar Blvd. and Balentine Dr., Newark, Alameda Co., CA.

Reason	No. Owls	Season	Nearest Habitat
Development	4	Fall	<760 m away

Owls flushed from site (20 Sept. 1990) and nest burrows were excavated prior to disking the same day. One pair used depressions in ground for cover at the site after the burrow was destroyed. On 7 Oct. 1991 (last visit) one owl was seen at site of destroyed burrow.

Case 4. Mission College, Santa Clara, Santa Clara, CA.

Reason	No. Owls	Season	Nearest Habitat
Development	12	Summer	<150 m away

Burrows excavated and closed 10 Aug. (year not provided). One pair remained near destroyed burrow at the construction site until the last visit on 21 Aug. of the same year. Another pair moved to another burrow about 500 ft away. A single adult and seven juveniles were not observed again.

Relocation

Case 1. Cushing Parkway and Northport Drive, Fremont, Alameda Co., CA.

Reason	No. Owls	Season	Distance Relocated
Unknown	3	Fall	<19 km

Kept in aviary at new site from 30 Oct.–7 Nov. 1989 when they were released. On 14 Nov. only one owl remained at relocation site and it stayed until at least 22 Nov. 1989.

Case 2. Mission College, Santa Clara, Santa Clara Co., CA.

Reason	No. Owls	Season	Distance Relocated
Development	10	Late winter	Approximately 30 km

Kept in aviary at new site from 3–4 Mar.–15–16 Mar. 1990, when they were released. Found missing on 6 Apr. and 24 May 1990. Three pairs returned to original site; 6–8 June 1990, 19 July 1990, 7 Aug. 1992. One male owl, which was relocated to new site remained at that site until at least August of 1992.

Case 3. San Jose, Santa Clara Co., CA.

Reason	No. Owls	Season	Distance Relocated
Unknown	1	Fall	Approximately 40 km

Taken to relocation site 30 Apr. 1986 and found back at the original site 27 May 1986. Bird was retrapped in summer of 1987 and released in Cholame, San Luis Obispo Co., CA about 200 mi south of original site. It was not seen again.

Case 4. South San Jose, Santa Clara Co., CA.

Reason	No. Owls	Season	Distance Relocated
Development	2	Spring	Approximately 32 km and 64 km

Taken to relocation site 30 Apr. 1986. Found at original site on 3 June 1986 at a burrow near original burrow with 5 eggs. Birds recaptured and rereleased 40 mi south of original site. They were not known to return.

Case 5. Mountain View, Santa Clara Co., CA.

Reason	No. Owls	Season	Distance Relocated
Rescue	1	Fall	45 km

Rescued from stairwell and released 21 Nov. 1985. Bird found back near original location; date not provided.

Case 6. Coronado Island Naval Air Station, San Diego, San Diego Co., CA.

Reason	No. Owls	Season	Distance Relocated
Predation	2	Breeding	48 km

Burrowing owls taking least tern (*Sterna antillarum browni*) young; relocated owls to the north, and they were back at the original site the same day.

Case 7. Coronado Island Naval Air Station, San Diego, San Diego Co., CA.

Reason	No. Owls	Season	Distance Relocated
Predation	2	Breeding	48 km

Burrowing owls taking least tern young; relocated owls to the east, and they were found at the original site when biologist returned on the same day.

Case 8. Coronado Island Naval Air Station, San Diego, San Diego Co., CA.

Reason	No. Owls	Season	Distance Relocated
Predation	4	Breeding	>144 km

Burrowing owls taking least tern young; relocated owls to the east at Anza Borrego State Park, San Diego Co., CA and Salton Sea National Wildlife Refuge, Imperial Co., CA. Relocation site now provided a 5000 ft mountain range barrier to original site. Owls did not return to original site.

Case 9. Bay Farm Island, Alameda, Alameda Co., CA.

Reason	No. Owls	Season	Distance Relocated
Development	4	Fall	<1.6 km

Two wild and two rehabilitated burrowing owls were banded and kept in an aviary for 5 d at new location (November 1986). One bird was seen at the relocation site sporadically for the first two weeks after release, then disappeared. Another owl was found nesting at original site in April 1987 with an unbanded mate. The two rehabilitated owls stayed at the relocation site and brought unbanded mates to the artificial burrows by the end of December 1986.

Case 10. Moses Lake Area, Grant Co., WA.

Reason	No. Owls	Season	Distance Relocated
Translocation	55	Summer	Approximately 240 km

Ten adults and 45 hatchlings relocated to Osoyoos Lake, British Columbia (BC). Most adults dispersed from the release site by the end of the first week, July 1985. Thirty-eight juvenile owls fledged and all dispersed September 1985. In March of 1987 one owl released in BC was recovered at original trapping site in Washington. A second banded bird at original site was presumed to be a returned transplanted bird. Other adults have since returned to Washington. Transplanted hatchlings had not been observed returning to Washington as of October 1992.

Discussion

Contributors to the above cases offered suggestions for the burrowing owls' resistance to leaving an area or to their returning to an original site location: (1) there may be a bond to an active nest and/or home territory; (2) breeding success or simply survival at the original site for one or more years is thought to intensify the territorial bond; (3) attachment to a mate and/or colony social structure may be a consideration for territorial bonding; (4) low or unfamiliar prey base at new location may cause site rejection; (5) the presence of predators at the new location can cause direct risk to the owls or competition for prey and abandonment; (6) unfamiliar disturbance(s) can intimidate owls at a new location; and (7) there may be potential for errors at the new location in artificial habitat strategies, such as the design and/or placement of artificial burrows.

The tendancy to reuse an established breeding site has been recorded for a wide variety of avian species (McNicholl 1975, Shields 1984, Atwood and Massey 1988, Dobkin et al. 1986). Numerous studies have shown that reproductive success influences the continued use of avian breeding sites (Freer 1979; Harvey et al. 1979; Burger 1982; Newton and Marquiss 1982; Oring and Lank 1982; Redmond and Jenni 1982; Calder et al. 1983; Dow and Fredga 1983; Burger 1984; Shields 1984). It has also been shown that familiarity with habitat surroundings and neighboring individuals reduces risks with at least larids (McNicholl 1975).

Predation of burrowing owls at new sites has been documented. A burrowing owl relocation project in Minnesota resulted in a great horned owl (*Bubo virginianus*) causing the loss of all relocated burrowing owls (Dyer 1987). Great horned owls have also taken young peregrine falcons (*Falco peregrinus*) reintroduced to natural cliffs along the east coast of the United States (Newton 1979).

Tengmalm's owls (*Aegolius funereus*) avoided nest boxes or natural holes in which they suffered predation the previous year, suggesting that predation can cause nest site abandonment for this owl (Sonerud 1985).

The need for additional information to help determine the best strategies for successful burrow closure and relocation projects points to the importance of careful long term monitoring and sharing of results.

There will be more development, and biologists will continue to get calls to move burrowing owls for one reason or another. The above-mentioned references suggest that site tenacity is very likely a mechanism designed to assist birds in survival and breeding success. Coaxing burrowing owls to overcome site tenacity during burrow closure and relocation projects will have a greater chance of success if we have a thorough understanding of the ecological details of the original and relocation sites and the life histories of the owls involved. With this information in hand, we can design more successful relocation schemes.

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RELOCATION OF BURROWING OWLS DURING COURTSHIP PERIOD

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ABSTRACT.—Five pairs of burrowing owls (*Speotyto cunicularia*) were relocated from a site in Santa Clara, California, to two sites located approximately 31 km to the south, in March 1990. Ten owls were trapped in mid-February and released from hacking aviaries in mid-March three to four weeks after capture. We supplemented food from the date of capture, and the amount of food was gradually diminished to zero over time. We monitored local movements of the ten owls. Two pairs of owls bred successfully at each of the two relocation sites (STL and ARC). One of these produced six nestlings, at least two of which survived to fledging. The second pair produced eggs and young, but the nest failed due to predation. Two other pairs attempted breeding (i.e., nest construction), but the male of one pair was killed by a predator prior to the egg-laying stage and the second pair left the site. Three female owls, all of which had experienced a failed nesting attempt, left the relocation sites and returned to the capture site. Six owls remained at the STL site in 1991, and two owls were still present in 1992. A pair of owls attempted to nest at the ARC site in 1991, and at least one owl has been observed at the site through 1994. Although the relocation sites were to be managed in the long term for burrowing owls, these management plans were not followed, and owls generally dispersed by the end of 1991. This study indicates that burrowing owls may be successfully relocated if birds are moved at the beginning of the breeding season.

KEY WORDS: *burrowing owl*; Speotyto cunicularia; *relocation*; *courtship period*; *hacking*; *California*.

Relocalizacion de tecolotito enano durante el periodo de cortejo

RESUMEN.—Cinco pares de tecolotito enano (*Speotyto cunicularia*) se relocalizaron de un sitio en Santa Clara, California, a dos sitios aproximadamente 31 km al sur en marzo de 1990. Diez tecolotes se atraparon a mediados de Febrero y se liberaron de aviarios a mediados de marzo tres y cuatro semanas despues de captura. Se suplemento la alimentacion de las aves desde el dia de captura, y la cantidad de alimento se redujo gradualmente hasta zero. Monitoreamos movimientos locales de los diez tecolotes. Dos parejas de tecolotes se reproducieron exitosamente en dos sitios de relocalizacion. Una pareja produjo seis polluelos dos de los cuales sobrevivieron hasta volantones. El segundo par produjo huevos y pollos pero el nido fallo debido a depredacion. Otras dos parejas atentaron reproduccion (construyeron nidos) pero el macho de un par fue matado por un depredador antes de la postura de huevos y el segundo par abandono el sitio de recolonizacion y regresaron al sitio de captura. Seis tecolotes permanecieron en el sitio de relocalizacion en 1991 y dos tecolotes estaban presentes en 1992. Un par de tecolotes atentaron anidar en el sitio hasta 1994. Aunque los sitios de relocalizacion deberian de haberse manejado a largo plazo para los tecolotitos enanos estos planes de manejo no se siguierion y los tecolotes se dipsersaron para fines de 1991. Este estudio indico que los tecolotitos enanos pueden ser relocalizados exitosamente si se mueven a principios de la epoca reproductiva.

[Traducción de Filepe Chavez-Ramirez]

The burrowing owl (*Speotyto cunicularia*) is a small, terrestrial owl noted for its ability to coexist with humans in a variety of urban and semi-urban environments.

Once common, or even abundant locally, burrowing owls have declined over the last few decades throughout much of California (Grinnell and Miller 1944, McCaskie et al. 1979, Garrett and Dunn 1981). Population declines have been attributed to land development, cattle ranching, control of rodents, prairie dogs (*Cynomys* sp.), badgers (*Taxidea taxus*), and other burrowing animals, and vehicle strikes (Martell 1990, K. McKeever pers. comm.).

One potential solution to avoid increasing impacts to owls has involved relocating owls from impact areas to appropriate habitat elsewhere. Active relocation refers to physically trapping and moving owls from one location to another. Some relocations have been successful in that viable populations have been established (Dyer 1991).

Of eight previous relocations in California, three occurred in the fall, two in the spring, and the time of year is unknown for the other three (Feeney 1993). Of the three fall relocations, only one (using hacking aviaries) was moderately successful, with two of six owls remaining and breeding on site for up to three years (Harris 1987). Birds released during two spring relocations returned to the original site within one month of release (Feeney 1993). My study was designed to test the hypothesis that the timing of relocation may strongly influence whether birds stay on a relocation site.

METHODS

The capture site was a 24.3-ha parcel of land owned by the Mission College Foundation. The parcel will potentially be developed and is adjacent to busy freeway and surface streets in Santa Clara, California (Fig. 1).

A survey was conducted in December 1989 at the Mission College site to determine the number of owls to be trapped and the locations of their burrows. Two sites approximately 31 km to the south of the capture site were selected for relocating birds. These sites were on property owned by IBM Corporation, and both were designated as open space. One of the two sites is at the Santa Teresa Laboratory (STL), a 48.5-ha portion of a 478-ha parcel of land located north of Bailey Avenue and west of Highway 101. The second site, the Almaden Research Center (ARC) is a 280-ha parcel near Bernal Road. The relocation site at STL, at an elevation of 76 m, in the Santa Teresa Hills, is at the edge of an alluvial flood plain bordered to the southwest by oak woodland and to the southeast by agricultural fields. The site is valley grassland modified by agriculture. Prune and almond trees occupy part of the eastern and northeastern portion of the agricultural area. During the study, the site was managed as a hayfield, and red oats (*Avena* sp.) were planted in November and harvested in May. Following the harvest, the field was disked and left fallow between June and November. The herbicide 2,4-D was used on the crop to kill broadleaf weeds and field mustard (*Brassica rapa*). The farmer also hired a licensed pest control specialist on a yearly basis during the summer to control ground squirrels on the property. The specialist placed gas pellets (fumigants) in burrows, which were then closed. The farmer agreed not to control the ground squirrels in 1990 to prevent potential harm to burrowing owls (R. Lester pers. comm.). The ARC site, at an elevation of 256 m, is on serpentine rock, and contains grass species typical of serpentine grasslands. The site had been grazed by cattle continuously between the 1800s and 1987 (James A. Roberts Associates, Inc. undated). Although burrows of California ground squirrels (*Spermophilus beecheyi*) were present at both sites, artificial burrows were installed to provide additional nesting locations. Artificial burrows also provided a more controlled situation than ground squirrel burrows, whose configurations and occupancy could not be determined easily.

Santa Teresa Laboratory (STL). The area selected for nest sites is limited by agriculture. We set aside several sites with traditionally low yields for installation of artificial burrows and mounds. Artificial burrows generally followed the design described by Collins and Landry (1977). We installed four nest boxes approximately 3 m apart along a gently sloping hillside. Additional nest boxes were installed to allow for dispersal of owls following release. Each nest box was constructed from 2.5 cm thick redwood planks. The outside dimensions of each nest box were 40.6 cm × 30.5 cm × 30.5 cm, and the inside dimensions were 35.5 cm × 25.4 cm × 25.4 cm. The bottom of the box was open to the ground, and the top was secured by wood screws to allow for future observation and banding of nestlings. One 10 cm diameter hole was cut into the lower edge of two adjacent sides of each box. Two 10.2-cm diameter, 1.8 m long, corrugated, perforated PVC sewer drain pipes were fitted into each of the two holes in the box. Nest boxes were buried approximately 0.3 m below the ground surface, and 15–20 cm of dirt were mounded on top of each box. Hacking aviaries, with dimensions of 3 m × 3 m × 1.2 m, were constructed linearly with common walls. Aviary frames were made of 5 cm × 5 cm fir stakes. Heavy-duty black polyethylene marine netting (ADPI Enterprises Inc., Philadelphia, PA) with 1.2-cm mesh size was stapled to the sides and tops of frames. A feeding door, with dimensions of 41 cm × 51 cm was also secured to a top corner of each aviary. A section of 1.2 m wide chicken wire, folded in half, was attached to the sides of the aviaries from ground level up to a height of 0.6 m, then staked to the ground around the base of the aviaries. The chicken wire was intended to discourage mammalian predators, such as foxes (*Vulpes* sp.) or coyotes (*Canis latrans*) from digging under the aviary frames.

Twelve additional mounds were created in grassland. Mounds were spaced at least 31 m apart. Eight additional nest boxes were buried at ground level or above within dirt/debris mounds dumped along a grassy strip adjacent to Bailey Avenue. Four additional mounds were created with no nest boxes, to allow ground squirrels to create natural burrows.

Almaden Research Center (ARC). We installed a single artificial burrow and aviary with the same dimensions as those used at the STL (above) on the site at the base of a gently sloping hillside in the western corner of the agricultural area. Following a predator attack of the nest box in July, we reburied the nest box so that the top of the box was even with the ground surface. We secured the lid using wood screws and placed several large rocks on top of the earthen mound covering the nest box. We stretched heavy wire between tent stakes, which were driven into the ground on either side of the two plastic tunnel tubes to guard against further predation. The newly-strengthened nest box was tested the following day, when a predator unsuccessfully attempted to unearth the tubes. We installed two additional artificial burrows (each with one nest box) at the ARC site in early August to provide additional refugia for a second group of owls released on site. The nest boxes were 45–60 m from the original artificial burrow placed at that site.

Trapping. Between 15–21 February 1990 we placed noose carpets and Bal-chatri traps near burrows where pairs had been previously observed. Observers waited in vehicles at some distance and checked traps approximately once per half-hour. We removed captured birds immediately and placed them in standard cardboard pet carrying boxes.

Transfer to Rehabilitation Facility. We transported all captured owls to the Santa Clara Valley Humane Society. A rehabilitator experienced with burrowing owls examined each owl externally for parasites and diseases and tested a stool sample from each bird for internal parasites, such as *Capillaria*. Two of four owls captured carried feather lice (Laemobothriidae). One owl was treated for capillaria for 5 days, and one owl had infections on the toes and forehead which were treated with betadine and fenbendazole. We then transferred owls testing negative for internal parasites to another aviary for 13–15 d. We temporarily confined owls as an attempt to disrupt homing mechanisms prior to relocation. The approximate dimensions of the aviary were 3 m × 4.3 m × 2.4 m. We buried two nest boxes with approximate dimensions of 30–35 cm on a side in the ground with PVC tubes connecting them to the outside. We placed two perches along each of two sides of the cage, approximately 1.5 m above the ground. The inside walls and ground of the aviary had been disinfected with a solution of bleach and disinfectant prior to introducing the owls. We transferred three owls on 20 February and one owl on 22 February. We left live commercially-raised mice (B & K Universal, Fremont, CA) and crickets in the aviary daily and provided drinking water in a shallow bowl.

Relocation, Feeding, and Monitoring. We transferred owls to the two relocation sites on 5 March 1990, and placed each pair in a separate aviary for 10 d. We visited the site periodically to determine numbers and locations of owls at both sites, maintain burrows and provide supplemental mice. We removed old or rotting mouse carcasses from the immediate burrow entrances to avoid attracting predators to the site, collected regurgitated pellets during feeding visits, and periodically examined them to determine percentage of "wild" food the owls were procuring. We used this information to adjust the amount of supplemental food.

At the STL site, we supplementally fed the eight owls two mice per owl per day during the captivity period. After ten days, the hacking aviaries were removed, and owls were allowed to move freely. We left frozen mice inside burrow tunnel entrances to discourage predators, such as northern harriers (*Circus cyaneus*) from eating the mice. We fed and observed owls in the late afternoon, or evening, when they were most likely to be observed. We changed this feeding protocol after 10 April, when owls were observed feeding on mice during morning hours and were observed outside burrows at all times of the day. Two mice per owl per day were left for another five weeks, unless mice from a previous feeding were still present. We then fed owls three mice per pair for 12 d, followed by two mice per pair for one wk, and one mouse per pair every four d for a period of 20 d. The frequency of supplemental feeding increased to every other day when nestlings were discovered at one nest.

Additional Owl Releases. We relocated six additional owls on 21 June and released five fledged young on 19 September at the STL site. We also relocated six owls (three adults and three juveniles) to the ARC site on 7 August. All additional owls were hacked out in aviaries prior to release and fed in a similar fashion to the original five pairs.

Banding, Site Maintenance, and Follow-up Visits. We unearthed the four nest boxes at STL and one nest box at ARC on 15 March to determine nesting progress. We cleaned out unoccupied burrows and replaced nest box lids. One nest box was reopened on 5 June to band nestlings prior to their emergence from the burrow. We trimmed weeds growing around the four artificial burrows by hand and with a sickle bar mower (in June). The red oat crop was harvested in early May and the field was disked (excluding the burrow mounds). We revisited the STL site on 6 February 1991 to determine the number of owls remaining on the site. We visited the STL site on 11 April and the ARC site on 25 April 1992 to assess the number of owls on the sites and the integrity of the burrow sites.

RESULTS

Trapping Efficiency. The first group of six owls was captured at Mission College between 0545–1030 H on 15 February (trapping efficiency of 1 owl per 1.26 h). We captured four owls using noose carpets and two owls with Bal-chatri traps. We captured four additional owls on 21 February between 0530–0912 H. We captured two owls with Bal-chatri traps and two with noose carpets (trapping efficiency of 1 owl per 1.07 h).

Male-male interactions. Within one or two hours of their release from the aviaries, male owls from STL pairs 1, 2, and 3 were observed copulating with their mates. We also observed aggression between males of different pairs. Approximately 45 min after owls had emerged from burrows, the male of pair 2 attacked and briefly pinned the pair 1 male on the ground. The male of pair 1 subsequently attacked the pair 2 male after approximately 30 min. Fifteen min later, the males from pairs 2 and 3 were fighting. This pair engaged in another aggressive encounter approximately 65 min later.

Reproductive Success. Four of the five relocated pairs attempted breeding and produced eight nestlings and five eggs. At least two of the eight nestlings fledged at the STL site.

Pair 1 had begun lining its nest at artificial burrow A. When the nest box was checked on 15 May, some cut grass, cow dung, pellets, and 18 dead mice were found inside. The male, who had become relatively tame, was observed outside the burrow until at least 12 April. Owl feather remains were found near the burrow entrance on approximately 15 April and it is assumed that the male was killed by a predator. The female was observed at the original nest burrow until 18 April. Pair 1 remained at the relocation site longer than one month, and the female remained for an additional seven weeks.

Pair 2 originally occupied burrow B and remained there for more than one month. This pair used two burrows initially occupied by pair 4, and successfully nested. On 15 May, two months after release, four downy nestlings (approximately 10 cm in length), with eyes still closed, plus a single unhatched egg were observed in the burrow. We estimated that the young hatched between 9–17 May, and the four nestlings were between 2- and 4-d-old. By 5 June the female had laid a sixth egg, and all six young were banded with USFWS bands and colorbands. At least two of the young fledged and were observed on site through 24 August.

Pair 3 demonstrated breeding behavior (copulation) and remained at the relocation site for ten days following release. The pair was not observed thereafter.

Pair 4 initially occupied burrow D after release from the hacking aviary, but then moved to burrow F after two days, where they remained until 16 April (nearly four wk). We observed the pair using three adjacent artificial burrows (H, I, and J) south of the original four nest burrows. The pair showed evidence of courtship behavior and nest-building, but by 8 June, the female was often observed outside the burrow entrance, indicating that she was not incubating. The pair remained together through 21 July. The male of pair 4 joined a female who had been introduced to the site with 5 young on 21 June. The female returned to Mission College sometime during the next two years and was observed at that site with five young in 1992.

Pair 5 began foraging about two hours following release. The pair remained on site and successfully bred and produced three nestlings and five eggs. Two freshly killed meadow mice (*Microtus californicus*) were observed in the nest box. A predator (probably a coyote [*Canis latrans*]) dug up and opened the nest box one day after the nest check. The pair remained on site until 12 June, about one week following the destruction of their nest. The male remained on site for at least two additional months.

In 1991, one year following relocation, a pair of owls attempted to nest at the ARC site in a natural ground squirrel burrow (A. Erickson pers. comm.), and a single owl was also observed near the release site during May of that year. At least one owl has been reported at the ARC site in 1992, 1993, and 1994. The bird observed in fall of 1994 appeared to be a resident (vs. a migrant), due to the amount of whitewash and other signs around its three burrows (D. Hildebrand pers. comm.).

Mortality. Feather remains were found near the burrow of pair 1 on or about 15 April, and the male was assumed to have been killed by a predator. The day following a check of the nest box of pair 5 (ARC site) for nesting progress, a predator dug out the nest box, opened the lid and removed eggs and nestlings. The predator was likely a coyote or red fox (*V. vulpes*).

Dispersal. The pair 1 female, whose mate had been killed by a predator, was observed back at the Mission College site on 8 June, approximately 2.5 mo following release. She paired with a two-year-old (or older) male owl (banded in 1988), but did not breed in 1990. Pair 2 remained at the relocation site through the 1990 breeding season.

Pair 3 (from burrow C) began exploring burrow G after four days, although the male was still observed at the original burrow on the fourth day. The pair moved to and remained at burrow G until 25 March, 10 d following release but was not observed again. The plastic tunnel pipes to burrow G had been partially excavated by a ground predator on 23 March. Coyote scat was found near the burrow entrance on 27 March.

Pair 4 remained at the relocation site during 1990, but did not breed. The female was not observed after 21 July at the relocation site, but was later observed (in 1992) at the Mission College capture site.

The pair 5 female was observed at the Mission College site on 19 July (37 d after it was last observed at the ARC site). The female was observed two years later at Mission College (April–August 1992) with two fledged young. Her right eye was abscessed, possibly as a result of a foxtail (*Bromus* sp.) puncture. The female was later found at least 1.6 km from the site, where she had apparently been struck by a vehicle, and was transported to the Santa Clara Valley Humane Society. The bird eventually died of internal injuries.

The owls that remained at the STL relocation site, some of which could have been young of the

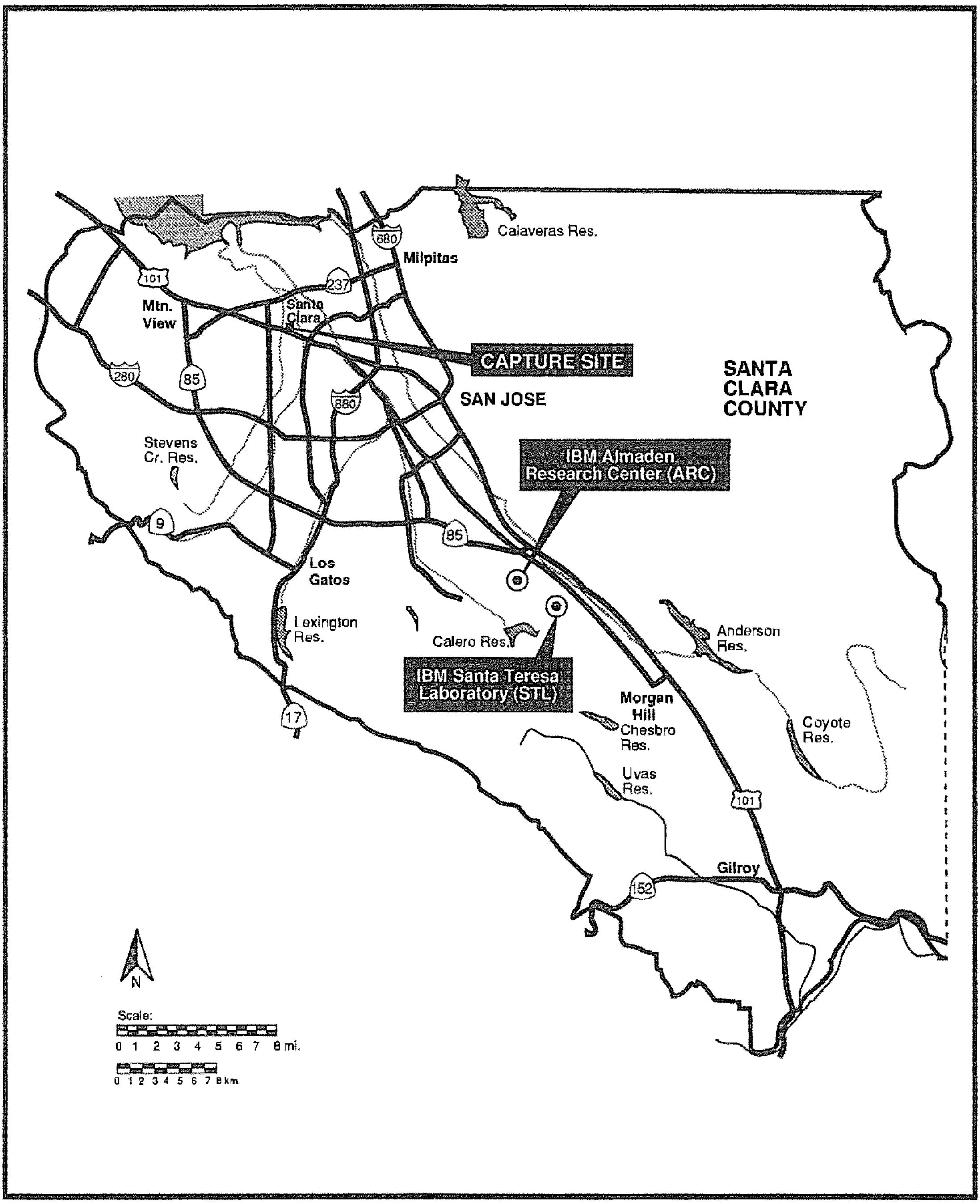

Figure 1. Location of capture site and relocation sites, San Jose, Santa Clara County, California.

above pairs, were supplementally fed through 29 November. The highest number of owls observed between September and November was six on 8 November. Two of the six appeared to be "paired."

DISCUSSION

This study represented one of the few attempts to relocate burrowing owls at the onset of the breeding season. Previous studies (e.g., Feeney 1997, H.T. Harvey and Associates 1993, Harris 1987) attempted relocation after the breeding season (primarily during the fall dispersal period). The most successful relocations to date involved moving dependent young with adults over a period of four to eight years (Dyer 1991). Four pairs of owls attempted breeding on site, and two pairs successfully produced young.

Even with the successful breeding of two pairs, there was some mortality and homing behavior. One male owl (pair 1) was killed by a predator. His mate returned to the Mission College capture site within two months of the male's death. The nesting failure of pair 5 was due to predation resulting from inadequate closure of the nest box. The female of this pair returned to Mission College within 28 d and bred the following season. Pair 2 produced 6 nestlings, of which at least two fledged. It is unclear how many, if any, survived to the following breeding season.

Two owls from STL and one owl from ARC returned to the relocation site within two years of release. All three were females who had failed at a nesting attempt, either through loss of eggs and young, loss of a mate, or unknown causes.

The STL site was not managed as habitat for burrowing owls. With proper habitat management, the owls would probably have persisted for a longer period and in higher numbers. Limited burrowing owl habitat was available at the ARC site, so only one pair of owls was initially moved to that site. However, it appears that at least one owl has remained at that site for four years. IBM Corporation had intended to follow a habitat management plan, which included plans for enhancing the STL site for burrowing owls. However, due to unforeseen circumstances, IBM was not able to follow the management plan. The agricultural regime of planting, harvesting, and disking that had been practiced for several years was continued during the study period. As previously noted, the site was disked and left fallow between June and November, the period when nestlings and fledglings would require the most amount of food for growth. The owls may have moved off site due to the lack of food during the critical nestling and fledgling period. The productivity of the land also may have been too low to support a large population of owls.

Methods for reducing territorial interactions need to be examined. Although additional artificial burrows were installed around the perimeter of the habitat available for owls, the artificial burrows at the STL site were placed too close to one another. This probably enhanced initial defensive encounters between males. Two males exhibited aggressive interactions on the first day of release from aviaries. Two pairs moved away from the original four-burrow complex to nearby burrows.

The selection and preparation of new nest burrows, and holding birds in captivity probably delayed the onset of egg-laying. Future relocations should consider decreasing the period in captivity, and increasing the distance between artificial burrows to at least 60 m (average of internest distances reported by Thomsen 1971).

We fed the owls more mice than necessary. Observers were not aware that owls were storing mice in large quantities until nest boxes were opened. The relocated birds from STL stored a large number of laboratory mice during 2.5 mo. One burrow contained 102 decaying mice, and five burrows contained 259 mice. Caching large quantities of food items may have attracted predators to the site. Reduction in the supplemental feeding may reduce predation.

The relocated owls also may have experienced unfamiliar predators, such as coyotes, red foxes, striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), bobcats (*Lynx rufus*), and gopher snakes (*Pituophis catenifer*), although red-tailed hawks (*Buteo jamaicensis*) and feral cats were common predators at the Mission College site.

In conclusion, relocations can work with improved techniques. This study demonstrated that birds moved prior to the initiation of egg-laying will breed successfully and remain at a new site less than 32 km distant. With proper land management, relocated birds may be able to sustain viable populations. Future research should focus on relocation site suitability and possible ways to reduce predation.

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I wish to thank the following persons for their advice, help in trapping and relocating owls, or for intermediate facilities: Craig Kuziel and Colleen Lenihan for their talents during aviary construction and trapping; Joan Priest and Jean Young for their care and treatment of the owls; and Janis T. Buchanan, Armand Gonzales (CDFG), Brenda Johnson, Susan Lyman, Ray Lester, Richard Reisman, Elsie Richey, Ken Ryan, Scott B. Terrill, and George Wade. I would also like to thank the following volunteers from IBM ARC and STL for giving so freely of their time and enthusiasm: Matt Anderson, John Artim, Perry Babel, Sheila Barclay, Irene Beardsley, Brenda Brown, Ray Dias, Rich Ehrhart, Allyn Erickson, Earl Hames, Dave Hildebrand, Mary Lehner, Dave Lopez, Bill Lundgren, Alan Neal, Dieter Thiel, Tom Maxson, Lance Porter, Berne Schoonmaker, Rick Stees, Stanley Taylor and Gloria Thompson. I am grateful to IBM Corporation for providing a relocation site, funds and manpower for building aviaries, and providing feeder mice. I also wish to thank Scott Terrill, Michael Newcomer, Karen Steenhof, and Jeff Lincer for reviewing the paper and providing helpful comments.

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APPENDIX A

A BIBLIOGRAPHY ON THE BURROWING OWL (*SPEOTYTO CUNICULARIA*)

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BACKGROUND

One might ask, in this day and age of electronic information retrieval, why we are producing a hard copy of a bibliography on just a single species of owl? We offer in reply, that even though professional researchers within university systems or within governmental agencies in the industrial world may have access to such "necessities," for much of the rest of the world that is still a luxury beyond the reach of those who could make use of it. The burrowing owl (*Speotyto cunicularia*) is found throughout much of the Western Hemisphere from southcentral and southwestern Canada to Tierra del Fuego. While the range of the race found in Florida (*floridana*) has been expanding due to forest clearing and draining activities, there are numerous other places where the species is declining. Because it is so "tied to the land" with its nesting habitats, this trend could reasonably be expected to not only continue but even increase at a greater rate as the human population continues to increase and agricultural practices intensify to feed the burgeoning human population. It is for these and other reasons that this bibliography was produced to assist researchers in uncovering the basic biology of this species and land managers in devising plans that can maximize the conservation of this species. Thus far, two races of the species have been eliminated (i.e., *guadeloupensis* from Guadeloupe and/or Marie Galante Island and *amaura* from Antigua in the West Indies). Both disappeared at the end of the nineteenth century at about the same time and shortly after the introduction of the mongoose by man (Greenway 1967).

METHODS

One should note that no bibliography is ever complete. All known and available literature databases and bibliographies have been searched. The databases include those information systems of the Raptor Research and Technical Assistance Center (RRTAC) created by Richard Olendorff, Karen Steenhof and others and **The Field Ornithology Index** (years 1984 through mid-1990 obtained on diskettes from the compiler John Kennington of Tulsa, Oklahoma). The **Science Citation Index** (January 1985–June 1992), **Dissertation Abstracts** (1861–June 1992), **Periodical Abstracts** and **Newspaper Abstracts** were all searched (from CD-ROM) at the Science Library, University of Kansas Libraries, Lawrence. Also searched via Lockheed's **Dialog** were **Biosis Previews, Books in Print, Life Science Collections, SciSearch** and **Zoological Record** by Bill Markle, Reference Librarian for York College of Pennsylvania. Bibliographies checked included those by Clark, Smith and Kelso (1978), Dunbar (1982), Knight (1979) and Olendorff (1989). Abstracts for Raptor Research Foundation annual conferences were checked for the years 1977–1992. Journal title abbreviations were taken from *Serial Sources for the BIOSIS Previews®*, Volume 1991.

It is our intent to produce a working bibliography; that is, one that is cross-referenced at a later date; hence, there is still ample time for those who know of other appropriate references. Especially helpful are reprints which allow some form of keywording to be created. Please send them to: Richard J. Clark, Burrowing Owl Bibliography, c/o Department of Biology, York College of Pennsylvania, York, PA 17405-7199 U.S.A.

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ing owl or *Speotyto cunicularia* or *Athene cunicularia* appeared in the title and/or the keywords of that specific article. A grant from the Research and Publications Committee of York College of Pennsylvania's Faculty Senate is hereby gratefully acknowledged, as is support from Biosystems Analysis, Inc. and Sweetwater Environmental Biologists, Inc.

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APPENDIX B

BURROWING OWL SURVEY PROTOCOL AND MITIGATION GUIDELINES

Prepared by:
The California Burrowing Owl Consortium

Editor's Note: The California Burrowing Owl Consortium prepared the "Burrowing Owl Survey Protocol and Mitigation Guidelines" in response to the need for more uniform methods of conducting owl surveys and to promote more consistent procedures in mitigating impacts to burrowing owls from development projects. The Consortium is a group of approximately 60 biologists and citizens interested in burrowing owl conservation and management in the San Francisco Bay area. This document was submitted to the California Department of Fish and Game (CDFG) for review and to any interested party who requested information regarding survey methods or mitigation strategies. For more information, updates, or to provide input to these evolving guidelines, contact: Mr. Jack Barclay, BioSystems Analysis, Inc., 303 Potrero Street, Suite 29-203, Santa Cruz, California 95060, (408) 459-9100. For information on CDFG's Staff Report on Burrowing Owl Mitigation guidelines, please contact Mr. Ron Rempel, CDFG, 1416 9th Street, Room 1341, Sacramento, California 95814, (916) 654–9980.

Background

The California Burrowing Owl Consortium developed the following Survey Protocol and Mitigation Guidelines to meet the need for uniform standards when surveying burrowing owl (*Speotyto cunicularia*) populations and evaluating impacts from development projects. The California Burrowing Owl Consortium is a group of biologists in the San Francisco Bay area who are interested in burrowing owl conservation. The following survey protocol and mitigation guidelines were prepared by the Consortium's Mitigation Committee. These procedures offer a decision-making process aimed at preserving burrowing owls in place with adequate habitat.

California's burrowing owl population is clearly in peril and if declines continue unchecked the species may qualify for listing. Because of the intense pressure for development of open, flat grasslands in California, resource managers frequently face conflicts between owls and development projects. Owls can be affected by disturbance and habitat loss, even though there may be no direct impacts to the birds themselves or their burrows. There is often inadequate information about the presence of owls on a project site until ground disturbance is imminent. When this occurs there is usually insufficient time to evaluate impacts to owls and their habitat. The absence of standardized field survey methods impairs adequate and consistent impact assessment during regulatory review processes, which in turn reduces the possibility of effective mitigation.

These guidelines are intended to provide a decision-making process that should be implemented wherever there is potential for an action or project to adversely affect burrowing owls or the resources that support them. The process begins with a four-step survey protocol to document the presence of burrowing owl habitat, and evaluate burrowing owl use of the project site and a surrounding buffer zone. When surveys confirm occupied habitat, the mitigation measures are followed to minimize impacts to burrowing owls, their burrows and foraging habitat on the site. These guidelines emphasize maintaining burrowing owls and their resources in place rather than minimizing impacts through displacement of owls to an alternate site.

Each project and situation is different and these procedures may not be applicable in some circumstances. Finally, these are not strict rules or requirements that must be applied in all situations. They are guidelines to consider when evaluating burrowing owls and their habitat, and they suggest options for burrowing owl conservation when land use decisions are made.

Section 1 describes the four phase Burrowing Owl Survey Protocol. Section 2 contains the Mitigation Guidelines. Section 3 contains a discussion of various laws and regulations that protect burrowing owls and a list of references cited in the text.

We have submitted these documents to the California Department of Fish and Game (CDFG) for review and comment. These are untested procedures and we ask for your comments on improving their usefulness.

SECTION 1: BURROWING OWL SURVEY PROTOCOL

Phase I: Habitat Assessment

The first step in the survey process is to assess the presence of burrowing owl habitat on the project site including a 150-m (approx. 500 ft.) buffer zone around the project boundary (Thomsen 1971, Martin 1973) (Figure 1).

Burrowing Owl Habitat Description. Burrowing owl habitat can be found in annual and perennial grasslands, deserts, and scrublands characterized by low-growing vegetation (Zarn 1974). Suitable owl habitat may also include trees and shrubs if the canopy covers less than 30% of the ground surface. Burrows are the essential component of burrowing owl habitat: both natural and artificial burrows provide protection, shelter, and nests for burrowing owls (Henny and Blus 1981). Burrowing owls typically use burrows made by fossorial mammals, such as ground squirrels (*Spermaphilus beecheyi*) or badgers (*Taxidea taxus*), but also may use man-made structures, such as cement culverts; cement, asphalt, or wood debris piles; or openings beneath cement or asphalt pavement.

Occupied Burrowing Owl Habitat. Burrowing owls may use a site for breeding, wintering, foraging, and/or migration stopovers. Occupancy of suitable burrowing owl habitat can be verified at a site by an observation of at least one burrowing owl, or, alternatively, its molted feathers, cast pellets, prey remains, eggshell fragments, or excrement at or near a burrow entrance. Burrowing owls exhibit high site fidelity, reusing burrows year after year (Rich 1984, Feeney 1992). A site should be assumed occupied if at least one burrowing owl has been observed occupying a burrow there within the last three years (Rich 1984).

The Phase II burrow survey is required if burrowing owl habitat occurs on the site. If burrowing owl habitat is not present on the project site and buffer zone, the Phase II burrow survey is not necessary. A written report of the habitat assessment should be prepared (Phase IV), stating the reason(s) why the area is not burrowing owl habitat.

PHASE II: BURROW SURVEY

1. A survey for burrows and owls should be conducted by walking through suitable habitat over the entire project site and in areas within 150 m (approx 500 ft.) of the project impact zone. This 150-m buffer zone is included to account for adjacent burrows and foraging habitat outside the project area and impacts from factors such as noise and vibration due to heavy equipment which could impact resources outside the project area.

2. Pedestrian survey transects should be spaced to allow 100% visual coverage of the ground surface. The distance between transect center lines should be no more than 30 m (approx. 100 ft.), and should be reduced to account for differences in terrain, vegetation density, and ground surface visibility. To efficiently survey projects larger than 100 acres, it is recommended that two or more surveyors conduct concurrent surveys. Surveyors should maintain a minimum distance of 50 m (approx. 160 ft.) from any owls or occupied burrows. It is important to minimize disturbance near occupied burrows during all seasons.

3. If burrows or burrowing owls are recorded on the site, a map should be prepared of the burrow concentration areas. A breeding season survey and census (Phase III) of burrowing owls is the next step required.

4. Prepare a report (Phase IV) of the burrow survey stating whether or not burrows are present.

5. A preconstruction survey may be required by project-specific mitigations no more than 30 days prior to ground disturbing activity.

PHASE III: BURROWING OWL SURVEYS, CENSUS AND MAPPING

If the project site contains burrows that could be used by burrowing owls, then survey efforts should be directed toward determining owl presence on the site. Surveys in the breeding season are required to describe if, when, and how the site is used by burrowing owls. If no owls are observed using the site during the breeding season, a winter survey is required.

Survey Methodology. A complete burrowing owl survey consists of four site visits. During the initial site visit examine burrows for owl sign and map the locations of occupied burrows. Subsequent observations should be conducted from as many fixed points as necessary to provide visual coverage of the site using spotting scopes or binoculars. It is important to minimize disturbance near occupied burrows during all seasons. Site visits must be repeated on four separate days. Conduct these visits from two hours before sunset to one hour after or from one hour before to two hours after sunrise. Surveys should be conducted during weather that is conducive to observing owls outside their burrows. Avoid surveys during heavy rain, high winds (> 32 kmp), or dense fog.

Nesting Season Survey. The burrowing owl nesting season begins as early as 1 February and continues through 31 August (Thomsen 1971, Zarn 1974). The timing of nesting activities may vary with latitude and climatic conditions. If possible, the nesting season survey should be conducted during the peak of the breeding season, between 15 April and 15 July. Count and map all burrowing owl sightings, occupied burrows, and burrows with owl sign. Record numbers of pairs and juveniles, and behavior such as courtship and copulation. Map the approximate territory boundaries and foraging areas if known.

Survey for Winter Residents (non-breeding owls). Winter surveys should be conducted between 1 December and 31 January, during the period when wintering owls are most likely to be present. Count and map all owl sightings, occupied burrows, and burrows with owl sign.

Surveys Outside the Winter and Nesting Seasons. Positive results (i.e., owl sightings) outside of the above survey periods would be adequate to determine presence of owls on site. However, results of these surveys may be inadequate for mitigation planning because the numbers of owls and their pattern of distribution may change dur-

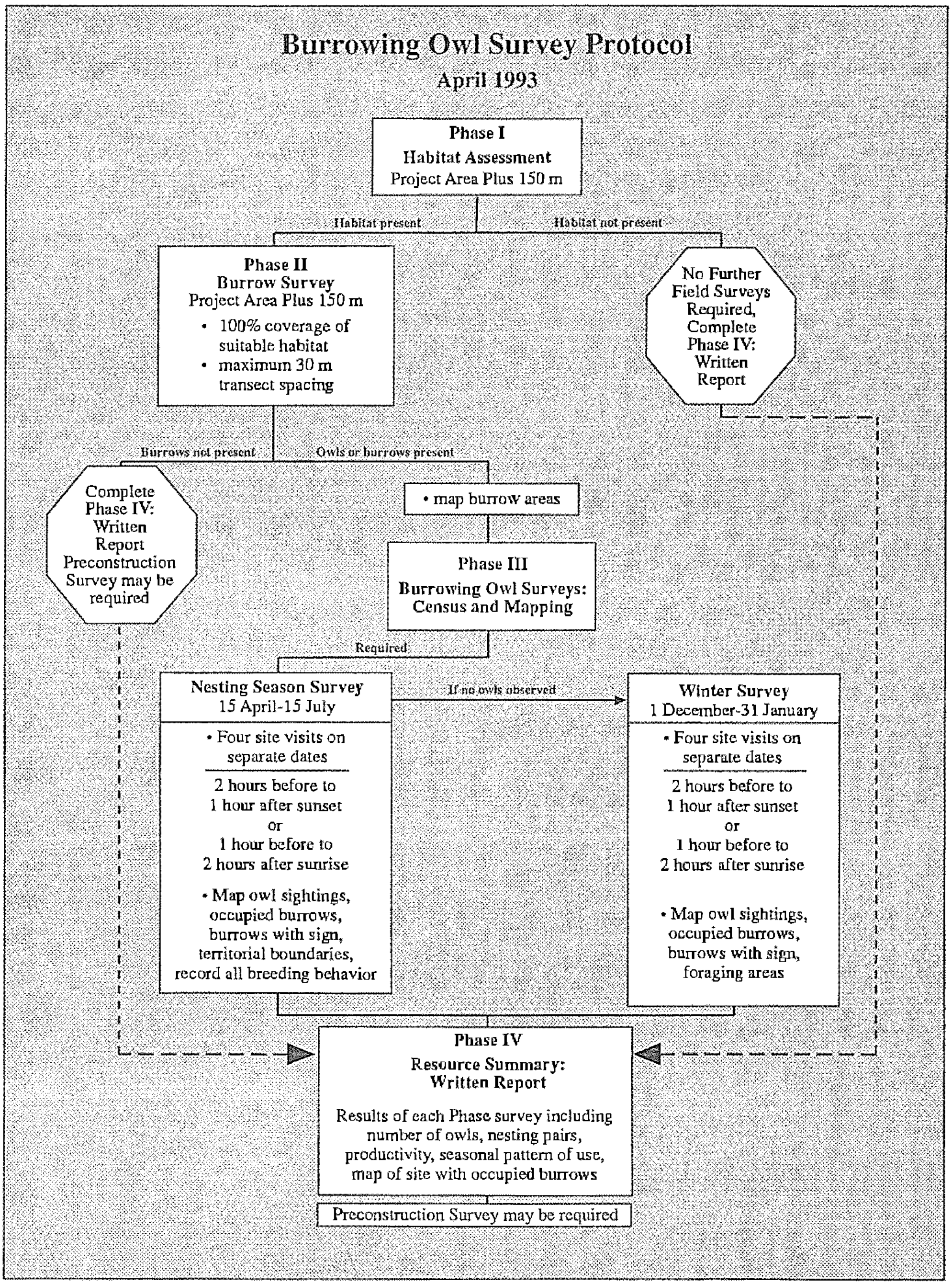

Figure 1. Burrowing owl survey protocol.

ing winter and nesting seasons. Negative results during surveys outside the above periods are not conclusive proof that owls do not use the site.

Preconstruction Survey. A preconstruction survey may be required by project-specific mitigations and should be conducted no more than 30 d prior to ground disturbing activity.

PHASE IV: RESOURCE SUMMARY, WRITTEN REPORT

A report should be prepared for CDFG that gives the results of each Phase of the survey protocol, as outlined below.

Phase I: Habitat Assessment

1. Date and time of visit(s) including weather and visibility conditions; methods of survey.
2. Site description including the following information: location, size, topography, vegetation communities, and animals observed during visit(s).
3. An assessment of habitat suitability for burrowing owls and explanation.
4. A map of the site.

Phase II: Burrow Survey

1. Date and time of visits including weather and visibility conditions; survey methods including transect spacing.
2. A more detailed site description should be made during this phase of the survey protocol including a partial plant list of primary vegetation, location of nearest freshwater (on or within 1.6 km of site), animals observed during transects.
3. Results of survey transects including a map showing the location of concentrations of burrow(s) (natural or artificial) and owl(s), if present.

Phase III: Burrowing Owl Surveys, Census and Mapping

1. Date and time of visits including weather and visibility conditions; survey methods including transect spacing.
2. Report and map the location of all burrowing owls and owl sign. Burrows occupied by owl(s) should be mapped indicating the number of owls at each burrow. Tracks, feathers, pellets, or other items (prey remains, animal scat) at burrows should also be reported.
3. Behavior of owls during the surveys should be carefully recorded (from a distance) and reported. Describe and map areas used by owls during the surveys. Although not required, all behavior is valuable to document including feeding, resting, courtship, alarm, territorial, parental, or juvenile behavior.
4. Both winter and nesting season surveys should be summarized. If possible include information regarding productivity of pairs, seasonal pattern of use, and include a map of the colony showing territorial boundaries and home ranges.
5. The historical presence of burrowing owls on site should be documented, as well as the source of such information (local bird club, Audubon society, other biologists, etc.).

SECTION 2: BURROWING OWL MITIGATION GUIDELINES

The objective of these mitigation guidelines is to minimize impacts to burrowing owls and the resources that support viable owl populations. These guidelines are intended to provide a decision-making process that should be implemented wherever there is potential for an action or project to adversely affect burrowing owls or their resources. The process begins with a four-step survey protocol (see *Burrowing Owl Survey Protocol*) to document the presence of burrowing owl habitat, and evaluate burrowing owl use of the project site and a surrounding buffer zone. When surveys confirm occupied habitat, the mitigation measures described below are followed to minimize impacts to burrowing owls, their burrows and foraging habitat on the site. These guidelines emphasize maintaining burrowing owls and their resources in place rather than minimizing impacts through displacement of owls to an alternate site.

Mitigation actions should be carried out prior to the burrowing owl breeding season, generally from 1 February through 31 August (Thomsen 1971, Zarn 1974). The timing of nesting activity may vary with latitude and climatic conditions. Project sites and buffer zones with suitable habitat should be resurveyed to ensure no burrowing owls have occupied them in the interim period between the initial surveys and ground disturbing activity. Repeat surveys should be conducted not more than 30 d prior to initial ground disturbing activity.

DEFINITION OF IMPACTS

1. Disturbance or harassment within 50 m (approx. 160 ft.) of occupied burrows.
2. Destruction of burrows and burrow entrances. Burrows include structures such as culverts, concrete slabs and debris piles that provide shelter to burrowing owls.
3. Degradation of foraging habitat adjacent to occupied burrows.

GENERAL CONSIDERATIONS

1. Occupied burrows should not be disturbed during the nesting season, from 1 February through 31 August, unless the Department of Fish and Game verifies that the birds have not begun egg-laying and incubation or that the juveniles from those burrows are foraging independently and capable of independent survival at an earlier date.
2. A minimum of 16 hectares of foraging habitat, calculated on a 100-m (approx. 300 ft.) foraging radius around the natal burrow, should be maintained per pair (or unpaired resident single bird) contiguous with burrows occupied within the last three years (Rich 1984, Fee-

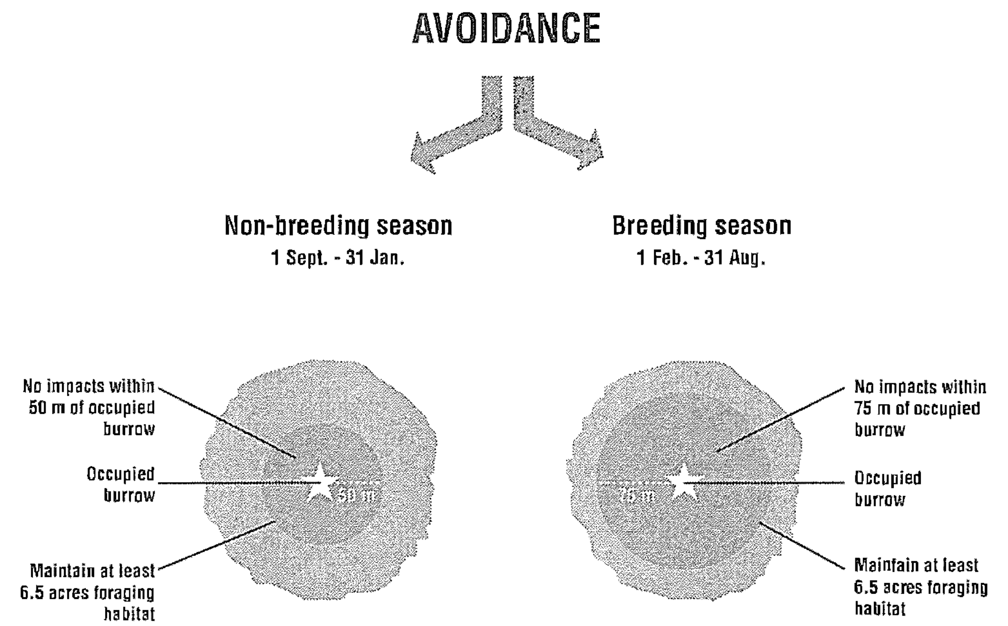

Figure 2. Avoidance area and necessary foraging habitat.

ney 1992). Ideally, foraging habitat should be retained in a long-term conservation easement.

3. When destruction of occupied burrows is unavoidable, burrows should be enhanced (enlarged or cleared of debris) or created (by installing artificial burrows) in a ratio of 1:1 in adjacent suitable habitat that is contiguous with the foraging habitat of the affected owls.

4. If owls must be moved away from the disturbance area, passive relocation (see below) is preferable to trapping. A time period of at least one week is recommended to allow the owls to move and acclimate to alternate burrows.

5. The mitigation committee recommends monitoring the success of mitigation programs as required in Assembly Bill 3180. A monitoring plan should include mitigation success criteria and an annual report should be submitted to the California Department of Fish and Game.

AVOIDANCE

Avoid Occupied Burrows. No disturbance should occur within 50 m (approx. 160 ft.) of occupied burrows during the non-breeding season of 1 September through 31 January or within 75 m (approx. 250 ft.) during the breeding season of 1 February through 31 August. Avoidance also requires that a minimum of 6.5 acres of foraging habitat be preserved contiguous with occupied burrow sites for each pair of breeding burrowing owls (with or without dependent young) or single unpaired resident bird (Figure 2).

MITIGATION FOR UNAVOIDABLE IMPACTS

On-site Mitigation. On-site passive relocation should be implemented if the above avoidance requirements cannot be met. Passive relocation is defined as encouraging owls to move from occupied burrows to alternate natural or artificial burrows that are beyond 50 m from the impact zone and that are within or contiguous to a minimum of 16 hectares of foraging habitat for each pair of relocated owls (Figure 3). Relocation of owls should only be implemented during the non-breeding season. On-site habitat should be preserved in a conservation easement and managed to promote burrowing owl use of the site.

Owls should be excluded from burrows in the immediate impact zone and within a 50 m (approx. 160 ft.)

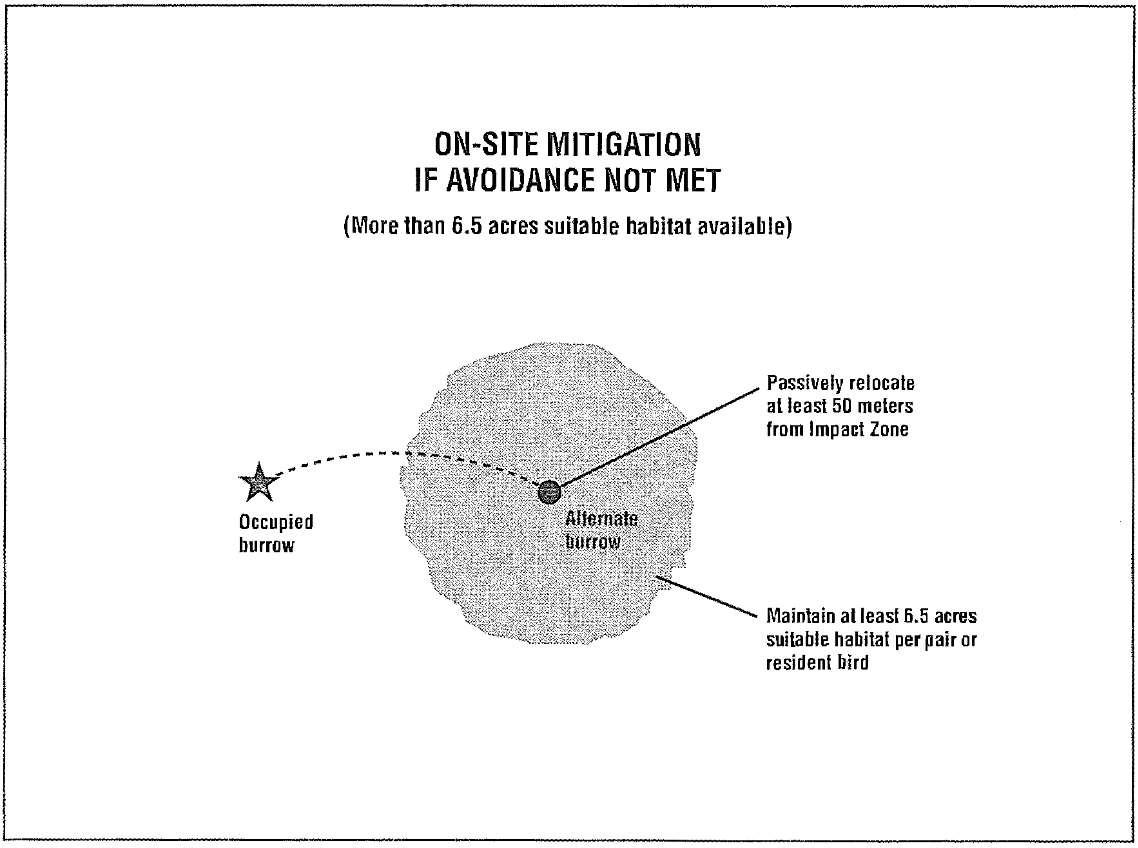

Figure 3. On-site mitigation.

buffer zone by installing one-way doors in burrow entrances. One-way doors should be left in place 48 h to ensure owls have left the burrow before excavation. One alternate natural or artificial burrow should be provided for each burrow that will be excavated in the project impact zone. The project area should be monitored daily for one week to confirm owl use of alternate burrows before excavating burrows in the immediate impact zone. Whenever possible, burrows should be excavated using hand tools and refilled to prevent reoccupation. Sections of flexible plastic pipe or burlap bags should be inserted into the tunnels during excavation to maintain an escape route for any animals inside the burrow.

Off-site Mitigation. If the project will reduce suitable habitat on-site below the threshold level of 6.5 acres per relocated pair or single bird, the habitat should be replaced off-site. Off-site habitat must be suitable burrowing owl habitat, as defined in the *Burrowing Owl Survey Protocol,* and the site approved by CDFG. Land should be purchased and/or placed in a conservation easement in perpetuity and managed to maintain suitable habitat. Off-site mitigation should use one of the following ratios:

1. Replacement of occupied habitat with occupied habitat: 1.5 times 6.5 (9.75) acres per pair or single bird.
2. Replacement of occupied habitat with habitat contiguous to currently occupied habitat: 2 times 6.5 (13.0) acres per pair or single bird.
3. Replacement of occupied habitat with suitable unoccupied habitat: 3 times 6.5 (19.5) acres per pair or single bird.

SECTION 3: LEGAL STATUS

The burrowing owl is a migratory bird species protected by international treaty under the Migratory Bird Treaty Act (MBTA) of 1918 (16 U.S.C. 703-711). The MBTA makes it unlawful to take, possess, buy, sell, purchase, or barter any migratory bird listed in 50 C.F.R. Part 10, including feathers or other parts, nests, eggs, or products, except as allowed by implementing regulations (50 C.F.R. 21). Sections 3503, 3503.5, and 3800 of the California Department of Fish and Game Code prohibit the take, possession, or destruction of birds, their nests or eggs. Implementation of the take provisions requires that project-related disturbance at active nesting territories be reduced or eliminated during critical phases of the nesting cycle (1 March–15 August, annually). Disturbance that causes nest abandonment and/or loss of reproductive effort (e.g., killing or abandonment of eggs or young) or the loss of habitat upon which the birds depend is considered "taking" and is potentially punishable by fines and/or imprisonment. Such taking would also violate federal law protecting migratory birds (e.g., MBTA).

The burrowing owl is a Species of Special Concern to California because of declines of suitable habitat and both localized and statewide population declines. Guidelines for the Implementation of the California Environmental Quality Act (CEQA) provide that a species be considered as endangered or "rare" regardless of appearance on a formal list for the purposes of the CEQA (Guidelines, Section 15380, subsections b and d). The CEQA requires a mandatory findings of significance if impacts to threatened or endangered species are likely to occur (Sections 21001(c), 21083. Guidelines 15380, 15064, 15065). Avoidance or mitigation must be presented to reduce impacts to less than significant levels.

CEQA and Subdivision Map Act

CEQA Guidelines Section 15065 directs that a mandatory finding of significance is required for projects that have the potential to substantially degrade or reduce the habitat of, or restrict the range of a threatened or endangered species. CEQA *requires* agencies to implement feasible mitigation measures or feasible alternatives identified in EIR's for projects which will otherwise cause significant adverse impacts (Sections 21002, 21081, 21083; Guidelines, sections 15002, subd. (a)(3), 15021, subd. (a)(2), 15091, subd. (a).).

To be legally adequate, mitigation measures must be capable of "avoiding the impact altogether by not taking a certain action or parts of an action"; "minimizing impacts by limiting the degree or magnitude of the action and its implementation"; "rectifying the impact by repairing, rehabilitating or restoring the impacted environment"; "or reducing or eliminating the impact over time by preservation and maintenance operations during the life of the action." (Guidelines, Section 15370).

Section 66474 (e) of the Subdivision Map Act states "a legislative body of a city or county shall deny approval of a tentative map or parcel map for which a tentative map was not required, if it makes any of the following findings:. . .(e) that the design of the subdivision or the proposed improvements are likely to cause substantial environmental damage or substantially and avoidably injure fish and wildlife or their habitat." In recent court cases, the court upheld that Section 66474(e) provides for environmental impact review separate from and independent of the requirements of CEQA (Topanga Assn. for a Scenic Community v. County of Los Angeles, 263 Cal. Rptr. 214 (1989).). The finding in Section 66474 is in addition to the requirements for the preparation of an EIR or Negative Declaration.

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