

THE ANCESTRAL KESTREL

Edited by
DAVID M. BIRD and
REED BOWMAN



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Preface

My feelings about kestrels are probably best summed up by the fact that I have bred in captivity over 1,500 of them, yet I still get that special thrill from watching a single wild bird hovering intently over a roadside ditch.

It is that same feeling which brought together about one hundred people to hear about "The Ancestral Kestrel" at a symposium on kestrel species on December 1, 1983 in St. Louis, Missouri. Twenty papers were presented in all, originating from kestrel experts from five countries. Naturally, the U.S. and Canada were the most heavily represented and hence, the symposium focused mainly on the American Kestrel (*Falco sparverius*). Since 1844, more than 450 articles have been published on the American Kestrel alone, 90 of which featured the species as an experimental animal. Although used somewhat less as a laboratory animal, similar statistics could likely be generated for the Eurasian Kestrel (*F. tinnunculus*).

According to **Douglas Boyce** and **Clayton White** in their lead paper on kestrel evolution and systematics, there are 15 species of kestrel world-wide, if one includes the Red-footed Falcons (*F. vespertinus* and *F. amurensis*). Moreover, the American Kestrel is perhaps the most recently evolved kestrel and is, in fact, the only New World representative of the kestrel's subgenus *tinnunculus*. Formerly known as the Sparrow Hawk, the American Kestrel is closely related to its old world cousin, the Eurasian Kestrel.

Mark Fuller, **Danny Bystrak**, **Chandler Robbins** and **Robert Patterson** examined trends in counts from the North American Breeding Bird Survey to conclude that the American Kestrel is the most common diurnal raptor throughout its range in North America.

Andrew Village of the U.K. reviewed published information on population regulation in kestrels to find considerable variation in dispersion patterns both within and between species. Possible mechanisms for population regulation within and outside the breeding season are suggested, along with experiments which might test their validity during the breeding season.

Paper themes then become more localized as **Carlos Wotzkow Alvarez** and **Jorge de la Cruz Lorenzo** of Cuba discuss their findings on the nesting success of the American Kestrel (*F. s. sparveroides*), a little studied race to date.

Another subspecies of American Kestrel, *F. s. paulus*, is featured in an article by **Mark Hoffman** and **Michael Collopy** who examined its distribution and nesting ecology near Archer, Florida. **Petra Bohall-Wood** also teams up with **Michael Collopy** to determine the foraging behavior of these same kestrels in relation to their habitat use.

As a more general follow-up to the latter paper, **Keith Bildstein** and **Michael Collopy** offer an excellent review of the literature on both American and Eurasian Kestrels to discuss their hunting behavior and success in light of current ecological thought. Stimulating suggestions for further research are also given.

Even more controversial is prey selection by kestrels. To this end, **Helmut Mueller** provides a rather lengthy, but thought-provoking critique of published results of both laboratory and field experimentation on prey selection, including his own extensive studies.

Two other current thorny issues are habitat separation by sex in wintering American Kestrels and reversed size dimorphism in birds of prey. **Ruthe Lash Meyer** and **Tom Balgooyen** tackle both these topics in their study of wintering American Kestrels in central California.

What all of the above really comes down to in the final analysis is the balance of energy gained and lost. **Dirkjan Masman** and **Serge Daan** of The Netherlands provide an excellent summary of their 700 days of continuous observation on Eurasian Kestrels throughout their annual cycle to determine allocation of energy. The annual changes in the daily use of energy were constructed for both sexes in terms of reproduction, moult and thermoregulation. They also discuss the energetic consequences of alternative behavioral patterns.

Their study is neatly followed by one on the energetics of the American Kestrel in northern Utah by **James Gessaman** and **Lucinda Haggas**. They computed daily energy expenditures for three different periods of the year: non-breeding, breeding, and post-breeding.

Next, **Reed Bowman**, **Jim Duncan** and **David Bird** delve into the behavioral ecology of the American Kestrel by examining data from four long-term banding projects across North America to estimate rates of natal philopatry and adult site tenacity.

Alan Kemp momentarily diverts our attention from the more common, well-known kestrels by presenting data on linear and weight measurements of mated pairs of Greater Kestrels (*F. rupicoloides*). He nicely ties the information together into discussions of reversed size dimorphism and biological fitness of individuals.

Despite the overwhelming success of nest box programs for kestrels around the world, there is always room for improvements. **Tom Wilmers** perused the literature to conclude that Starlings (*Sturnus vulgaris*), perhaps the kestrel's main competitor for nest sites, shun nest boxes with large entrances and high interior light levels. **Elizabeth Curley**, **Reed Bowman** and **David Bird** took Wilmer's ideas one step further by field-testing them. Indeed, Starling occupation can be reduced by decreasing the amount of cover above the boxes and by orienting the opening of the boxes such as to maximize light intensity in them.

Lastly, both American and Eurasian Kestrels breed readily in confinement, the former first bred in 1921 and the latter as early as 1850. Moreover, the American Kestrel was particularly valuable in helping to indict DDT as a significant cause of reproductive failure in wild birds. Both species of kestrel have actually contributed far more to the field of toxicology, as **Stanley Wiemeyer** and **Jeffrey Lincer** point out in their comprehensive review of the subject.

Beyond any doubt, both kestrel species will continue to make contributions toward the management and conservation of birds of prey, as well as toward avian biology in general. Books on both species are already in the works by Andrew Village and myself.

Each of the sixteen papers included in these proceedings was subjected to rigorous reviews by two referees and in some cases, an in-house review as well. Disagreements were resolved by a third referee. Additionally, each paper was scrutinized by two finicky editors, **Reed Bowman** and myself. If I had one misgiving about these proceedings, it would be the considerably long delay between the actual symposium and their publication. The reasons for this are not worth discussing here. In spite of the delay though, I am very confident that each paper has been adequately updated to provide fresh, original thinking on the subject.

The editors gratefully acknowledge the kind assistance of the following referees: **Tom Balgooyen**, **Keith Bildstein**, **Peter Bloom**, **Sandy Boyce**, **Michael Collopy**, **Serge Daan**, **Jim Enderson**, **Jim Gessaman**, **Charles Henny**, **Alan Jenkins**, **Roger Jones**, **Alan**

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Marie Kubecki is thanked for her assistance with word processing. I also extend my gratitude to the Department of Renewable Resources of McGill University for use of their facilities, to the Raptor Research Foundation, Inc. for allowing me to piggyback the symposium on their annual conference, and to Walter Crawford for being such a helpful host. Lastly, I offer special thanks to Shawn Farrell, Word Processing Consultant at McGill's Computing Centre, for introducing me to the world of PC \TeX , which added considerable polish to these proceedings.

DAVID M. BIRD

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EVOLUTIONARY ASPECTS OF KESTREL SYSTEMATICS: A SCENARIO

DOUGLAS A. BOYCE JR. and CLAYTON W. WHITE

Abstract: We suspect that one stock of ancestral Falconidae had its origin and early evolution in the Neotropics. We believe that a second (generalized?) stock, from which *Falco* was derived, occurred concurrently in the Old World, probably Africa and Southeast Asia. A major radiation of kestrels subsequently took place in Africa. We explore different models that might account for kestrel differentiation both within and between continental land masses. Pathways and time periods are evoked to explain the occurrence of a single species of kestrel in the New World, and these are speculated upon.

Kestrels fall into distinct color groups: gray forms and red-brown forms predominate. An intermediate group has plumage stages similar to both gray and red forms. Some species seemingly evolved *in situ* in Africa while the *tinnunculus*-like stock invaded north temperate areas. It is from the northern ones, by reinvasion into southern regions during the Plio-Pleistocene, that at least 4 *tinnunculus*-like species had their origin.

The gray African types, called "aberrant kestrels" by Cade (1982) (*F. ardosiaceus*, *F. zoniventris*, and *F. dickinsoni*), are probably more primitive than the "northern red form complex". The red-footed falcon types (*F. vespertinus* and *F. amurensis*), which may not be kestrels, may have been derived from an ancestral gray form. This derivation may help explain their winter migration to Africa from such distant regions as far eastern Asia.

The Family Falconidae

Current falconid interrelationships are based mainly on skeletal features. The falconid lineage is considered monophyletic and differs from other Falconiformes by virtue of 10 or more major features (Friedmann 1950, Jollie 1953, 1977). Some of these features are: vomerine bones that expand anteriorly; lachrymal bones without a superciliary plate; procoracoids articulating with the clavicle as well as with the scapula; eggshells having a reddish-yellow translucence rather than a greenish one; etc. In addition there are biochemical and behavioral differences. These traits unite very diverse genera [true falcons (*Falco*), "primitive" Neotropical groups including forest falcons (*Microcrastur*), Laughing Falcon (*Herpetotheres*), caracaras (*Polyborus*, *Daptrius*, *Milvago*, *Phalcoboenus*) and small to tiny falconets (*Microhierax*, *Polihierax*, *Spizapteryx*)] together in Falconidae.

The earliest falconid fossils are known from the middle Miocene [ca. 20 million years ago (MYA)] of Argentina and Nebraska (the New World) (Brodkorb 1964, Olson 1985). Of 11 fossil falconid species known through 1964, 2 were Miocene (with *F. ramenta* from the Miocene as the oldest *Falco*), 2 were Pliocene (ca. 3-12 MYA) and the remainder, Pleistocene (> 3 MYA). Eighteen contemporary living species are known from the Pleistocene (Brodkorb 1964), including 4 kestrels. A tiny "falconiform" from the Eocene of Europe has recently been found and tentatively assigned to Falconidae (Harrison 1982). It is of falconet size. While this Eocene fossil is not accepted as a falconid by Olson (1985), Mourer-Chauvers (1982) nonetheless list Falconidae from the Eo-Oligocene of France (ca. 30-45 MYA).

By Miocene (25-12 MYA) continental land masses were near their present positions (the continents, except Australia and India, were relatively close to present positions by

Paleocene, 65 MYA). Such a relatively late geological date for falconid appearance (30-45 MYA) is not parsimonious with the concept of a widespread group being separated onto various continents by vicariant events and then being carried with those continents as they drifted apart. Rather, classical dispersal, from some point of radiation, seems to explain current distribution of *Falco*. Therein lies a dilemma. Parsimony, in terms of current thinking, would suggest that different stocks were already on different continents as they drifted into their current geographical positions. However, we are taxed to make the time data fit because an earlier than Paleocene appearance of basic falconid stocks would be necessary to help solve the problem.

Recent egg white protein data (Sibley and Ahlquist 1972) and DNA-DNA hybridization data (C. Sibley and J. Ahlquist, pers. comm.) suggest that falconids evolved recently. The earliest neotropical falconid group diverged about 36 MYA ($T_{50}H$, 7.5-9.5). The Old World falconet *Microhierax* is older than *Falco* and in its divergence is similar to "caracaras" at about 28 MYA ($T_{50}H$, 6.1). *Falco*, as a group, is recent and diverged about 10 MYA ($T_{50}H$, 1.4-1.6, see Sibley and Ahlquist 1983 for explanation of aging methods). Old World falconets (*Microhierax*) (and also perhaps *Polihierax*?) are more closely related to *Falco* than are caracaras (J. Ahlquist pers. comm.). *Falco*, therefore, could have evolved from an Old World falconet (explaining their dominance there), while caracaras could have evolved from a falconet-like form in South America (perhaps *Spiziapteryx*-like?), and then *Falco* radiated and subsequently dispersed into the New World.

Current Systematics of the Genus *Falco*

Because it is not clear which genus in Falconidae is most ancestral (although we suspect a caracara-like *Daptrius*), we cannot be certain which species in *Falco* is oldest and retains pleisiomorphic characters. The entire family Falconidae awaits a comprehensive treatment like that given by Rae (1983) for vultures. *Falco* is so large and diverse that it is further broken into subgenera. Membership in *Falco* subgenera is based on bill proportions, leg and foot features, wing and tail proportions, feather characteristics, color, etc., and 7 subgenera are typically recognized. Of 39 species in *Falco*, 13 (33%) are considered to be kestrels (Cade 1982). Suschkin (1905), Brown and Amadon (1968) and Cade (1960, 1982) believed that kestrels are the most ancestral subgenus in *Falco* both in form and habit. If kestrels are indeed ancestral representatives in the genus, then small size, certain color traits, and body proportions are pleisiomorphic characters (see Table 1).

Kestrels, in the classical sense, are a group of small sized falcons generally assigned to the subgenus *Tinnunculus* or *Cerchneis* because of such shared traits as: long, more or less rounded tails (about 60% of length of wing); tarsi scarcely feathered on the upper portion and decidedly longer than the middle toe; and the inner and outer toes of similar length, with both being longer relative to the middle toe than other members of subgenera in *Falco*.

At least 2 species of kestrels, the Grey (*F. ardosiaceus*) and Dickinson's (*F. dickinsoni*) Kestrel, depart from the toe length generalization and along with the gray-colored Madagascar Banded Kestrel (*F. zoniventris*), have been placed in the subgenus *Disodectes*. It is because of the gray color and the usually double-toothed mandible that gray kestrels are allocated to a different subgenus (Snow 1978).

Brown and Amadon (1968) considered another "group", the Red-footed Falcons (*F. vespertinus* and *F. amurensis*), to be kestrels (thought by some to consist of only 1 species with 2 distinct races), but their position is certainly not clear and their morphology and

Table 1: Some ancestral (primitive?) traits and derived traits used in the analysis. 1. Adult plumages are derived and modified as secondary sexual characters for breeding and species recognition. 2. Sexual color dimorphism of adults in slight or non-existent in ancestral condition (as exists in many isolated island endemics); juvenile usually resemble females in cases where dimorphism exists and males diverge from the ancestral condition. 3. Eye color through the Falconiformes generally goes from a pale iris in accipitrids to dark iris in falconids though it may be variable within a given family or genus. Fossil record clearly shows accipitrids older than falconids. Dark iris is assumed to be derived. 4. Hovering flight is generally not found in accipitrids except in some with specialized hunting methods or some recent tundra-inhabiting forms. Hovering is believed to be derived.

Trait	General Accipitrid (outgroup)	Non- <i>Falco</i> Falconid	Non-Kestrel <i>Falco</i>	Kestrel
Plumage: <i>Juvenal</i> vs. <i>Adult</i>	<i>juv.</i> streaked, especially ventrally <i>ad.</i> variable, usually solid-colored venter	<i>juv.</i> many streaked or barred <i>ad.</i> variable, many with solid-colored venter	<i>juv.</i> streaked venter <i>ad.</i> variable	<i>juv.</i> streaked venter <i>ad.</i> variable
Sexual Color	slight or non-existent	slight or non-existent	slight or non-existent	most color dimorphic, some without
Eye Color	variable, most with pale iris	variable, many with pale iris	dark iris	dark iris, except one species
Hovering Flight	most non-hovering, specialized forms hover.	hovering not known dimorphism	hovering not known	most hover, some without

behavior is in some cases like hobbies and in other cases like kestrels (see also Brown et al. 1982). Stresemann and Amadon (1979) and Cramp and Simmons (1980) placed them sequentially following the gray African kestrels, but at the beginning of the hobbies. Red-footed falcons were placed in a separate subgenus, *Erythropus*, (literally meaning red foot) by Peters (1931) again adjacent to the 3 gray kestrels. Thus, there are 14 or 15 (38%) species of *Falco* that may be kestrels (*sensu lato*). In our discussion we consider the 2 red-footed forms to be separate species, following the assessment of Cade (1982), and we will clearly indicate when we include them in the analysis.

Definition of a Kestrel

One of the first questions to ask ourselves is “just exactly what is a kestrel?” When the word “kestrel” enters one’s mind it engenders many images. For some, it recalls days of medieval falconry when royalty allowed knaves or servants to use only kestrels and

thus made them unworthy of one's thoughts, much less one's steel. For others, it brings back pleasant memories. Watching the diminutive and delicate form plummet for prey, from a wire to the edge of a heavily travelled freeway, conjures images of wild and free in the midst of a bustling modern world. We suspect, however, most will only think of the American Kestrel (*F. sparverius*) or its European counterpart (*F. tinnunculus*) as typical kestrels. So closely do some kestrels resemble one another that, over a very large part of the globe, wherever travellers go, they are sure to meet a common raptor that in plumage and behavior reminds him of the kestrel in his own country. Kestrels have always been a favorite among ornithologists as evidenced by such appreciative literature comments as "the prettiest and jauntiest of our hawks" or "most light-hearted and frolicsome" (see Bent 1938).

Readers living in the New World may think of *F. sparverius* as a typical kestrel. But in terms of morphology it may not be an "average" or even "typical" kestrel. Let us derive a hypothetical kestrel from the data in Tables 2-3. We might develop what a statistician considers to be an average kestrel by calculating means. Such calculations reveal a falcon having a winglength of 225 mm, with a tail length of 145 mm, a tarsus 38 mm long, and a weight of 177 gm. This falcon would be inclined to hover while hunting and usually be found in open grassland savannah habitat.

Reviewing our list of kestrels, to locate the species most closely fitting the aforementioned mensural attributes, we notice that this falcon is not the American Kestrel but rather a little known falcon named Dickinson's Kestrel that occupies low-lying African savannahs. Moreover, *F. dickinsoni* does not have the typical red body color but is entirely gray and white! It is said to hover only occasionally; frequently individuals have a double toothed upper tomtia; and it is called an "aberrant kestrel" by Cade (1982) because of some morphological and behavioral traits. Clearly, Dickinson's Kestrel is not what most consider to be a typical kestrel.

The systematists' image of a kestrel, however, is a far cry from the average picture most carry in their minds. The pragmatic and scientifically dry constructs used by systematists, when examining museum skins of many different species to make sense of evolutionary forces that molded "kestrels", clashes directly with more poetic thoughts. The tiny and delicate feet and bill of the Lesser Kestrel (*F. naumanni*) compared to the robust and coarse feet and bill of the Grey Kestrel demand one, in an intellectual inquiry, to ask why the difference? The bright and contrasting color of *F. sparverius* or Seychelles Kestrel (*F. araea*) are in stark contrast to the dull, drab and uniformly slate gray color of *F. ardosiaceus*. Such color differences must have an evolutionary reason or meaning. It is with this latter pursuit, of talking about evolutionary relationships of kestrels, that we ask you to journey with us in our scenarios.

MATERIALS AND METHODS

Phylogenetic hypotheses were constructed using cladistic procedures (Eldredge and Cracraft 1980, Wiley 1981) on data sets of external morphological and behavioral characters. Continuous characters were gap-coded (Archie 1985). The Common Buzzard (*Buteo buteo*) and the Broad-winged Hawk (*B. platypterus*) were used as outgroups to generate hypotheses of character polarity. *Buteo platypterus* was selected because its size is closer to kestrels than is *B. buteo*. *Buteo* was selected as an outgroup because 1) Accipitridae is thought to be related to Falconidae, 2) Accipitridae is thought to be older than Falconidae, and 3) data were readily available for the characters selected. Characters were analyzed using the numerical cladistic program, Phylogenetic Analysis Using Parsimony (PAUP), written by David L. Swofford (1985 version 2.3). PAUP generated parsimonious trees that minimized the number of character transformations within the

Table 2: Wing length, tail length, and tarsus length (in mm) of both male (top figure) and female (bottom figure) kestrels^a. The number of races for each species is shown.

Species	Wing Length	Tail Length	Tarsus Length	Weight	# of races ^b
<i>F. tinnunculus</i>	230-266(244) 235-275(254)	150-174(162) 152-188(171)	37-43(41) 38-47(41)	111-152(196) 154-290(221)	11
<i>F. moluccensis</i>	205-233(219) 221-234(228)	(145) (?)	(42) (42)	?	6
<i>F. cenchroides</i>	237-255(246) 255-275(265)	(147) (157)	(38) (38)	162-170 (166) 160-192(178)	2
<i>F. sparverius</i>	174-198(183) 178-207(195)	116-142(129) 119-142(130)	34-42(38) 34-42(38)	109 119	14
<i>F. newtoni</i>	180-195(187) 188-203(195)	110-130(120) 115-131(122)	32-40(36) 32-40(36)	105 144	0
<i>F. punctatus</i>	162-182(172) 183-186(185)	126-135(130) (139)	38-45(41) (41)	178 231	0
<i>F. araea</i>	146-151(148) 152-156(154)	105-110(107) 103-115(109)	32-37(34.5) (34.5)	70 87	0
<i>F. naumanni</i>	227-247(234) 226-244(235)	133-148(140) 139-155(144)	30-33(31) 30-32(30)	120-155(148) 140-208(170)	0
<i>F. alopez</i>	266-293(280) 269-308(288)	180-212(196) 181-210(196)	43-44(43) 43-45(43)	? 224	0
<i>F. rupicoloides</i>	259-290(276) 265-294(281)	144-187(162) 144-187(162)	44-54(50) 44-54(50)	209-285(260) 240-295(272)	2
<i>F. ardosiaecus</i>	205-232(218) 235-251(242)	128-152(140) 150-164(157)	38-45(42) 40-47(43)	205-255(222) 240-250(247)	0
<i>F. dickinsoni</i>	210-236(223) 210-236(223)	128-152(140) 130-150(140)	35-38(36) 35-38(36)	167-246(210)	0
<i>F. zoniventris</i>	211-223(216) 219-234(226)	138-143(140) 144-152(148)	34-39(37) 34-39(37)	? ?	0
<i>F. vesperlinus</i>	224-255(240) 232-255(245)	119-135(127) 122-155(129)	28-31(29) 28-31(30)	115-169(156) 130-197(171)	0
<i>F. amurensis</i>	218-235(232) 225-242(234)	110-132(120) 111-132(121)	(28) (33)	97-155(136) 111-188(148)	0

^a Based on data from Brown and Amadon (1968), Cramp and Simmons (1980) and Brown et al. (1982).

^b Data from Stressemann and Amadon (1979).

data set (i.e., homoplasy is minimized) and generated minimum-length trees.

References used for data were Friedman (1950), Brown and Amadon (1968), Cramp and Simmons (1980) and Brown et al. (1982). Sexual size dimorphism in kestrels was eliminated by analyzing males separately from females. Four groups (G) were analyzed: (G1) males rooted to *B. platypterus*, (G2) males rooted to *B. buteo*, (G3) females rooted to *B. platypterus* and (G4) females rooted to *B. buteo*. Not all characters were shared between the taxonomic outgroup (T0G) and the taxonomic ingroup (T1G). Cladistic analysis requires that the T0G and the T1G share characters. In our analysis we began by using only synapomorphic characters (characters shared between T0G and T1G) to identify the species of kestrel most closely allied with the T0G (*Buteo*). Then, we used that species as our functional outgroup (F0G) to root to the remainder of kestrels (F1G). Rooting the F1G to the F0G allowed us to use the entire set of characters because all

characters were then functionally symplesiomorphic. We present only the most parsimonious hypothetical phylogeny from each group. Because of space constraints, tables of characters' synapomorphies will not appear here, but will be available by writing the authors. The character codes appear in Tables 4-7.

Table 3: General habitats and food and behavior of kestrels^a.

Species	General Habitat	Food	Hovers?
<i>F. tinnunculus</i>	open habitats or light woodlands; prefers open	80% insects	yes
<i>F. moluccensis</i>	low grass/shrub open country	small birds, mammals, lizards	yes
<i>F. cenchroides</i>	open forest and savannah	insects, birds, mammals	yes
<i>F. sparverius</i>	multiple habitats	insects, birds, mammals	yes
<i>F. neotoni</i>	open plains, sub-desert teppes; favors short grass plains	75% insects, birds, mammals, frogs	yes
<i>F. punctatus</i>	forest (now); open areas previously	insects, birds, lizards	no
<i>F. araea</i>	open and dense forest	lizards, insects	no
<i>F. naumanni</i>	open plains, sub-desert steppes; favors short grass plains	80% insects, lizards	yes
<i>F. alopez</i>	isolated rocky hills only	insects, mammals, no birds	no
<i>F. rupicoloides</i>	open grass plains and grass shrub; desert dotted with acacias	insects, mammals, reptiles (snakes)	yes
<i>F. ardosiaceus</i>	open grassland	insects, lizards, bats	yes
<i>F. dickinsoni</i>	low-lying savannahs, swampy flood plains, palms, coconut groves	insects, lizards, birds frogs and crabs	yes
<i>F. zoniventris</i>	tropical forests/edges savannah	insects, reptiles	rarely
<i>F. vespertinus</i>	grassland savannah, arid scrub, grassland	insects, mammals, reptiles	yes
<i>F. amurensis</i>	savannahs and grassland	insects, mammals, reptiles	yes

^a Based on data from Brown et al. (1982), Cade (1982), Cramp and Simmons (1980), and Brown and Amadon (1968).

RESULTS

Two phylogenetic trees were produced using *B. buteo* as the T0G (consistency index of .58) for males and 2 trees were produced using *B. platypterus* as the T0G (consistency index of .60). For females, 1 tree was produced using *B. buteo* as the T0G (consistency index of .57) and 29 trees were produced using *B. platypterus* as the T0G (consistency index of .60). Three T1G T0G analyses (G1, G3, G4) identified the Fox Kestrel (*F.*

Table 4: Character-state data for female kestrels in the genus *Falco* plus the outgroup (*B. buteo*). Character (character-state) key: 1) **Hovering**: (1) yes, (2) rarely, (3) no; 2) **wing size dimorphism**: (1) 3%, (2) 3.1-6.0%, (3) 6.1 + %; 3) **color dimorphism**: (1) uniform, (2) tail different, (3) bicolored; 4) **plumage change from juvenal to adult**: (1) no change, (2) male changes, (3) juvenal resembles male, (4) both sexes change; 5) **overall color**: (1 - 3) uniform to multicolored; 6) **eye color**: (1) dark, (2) pale; 7) **juvenal streaked**: (1) streaked, (2) solid, (3) variable; 8) **color**: (1) red, (2) gray, (3) red & gray; 9) **mean wing length**: (1) 398 mm, (2) 223-288 mm, (3) 154-195 mm; 10) **minimum wing length**: (1) 374 mm, (2) 178-269 mm, (3) 152 mm; 11) **maximum wing length**: (1) 419 mm, (2) 156-308; 12) **mean tail length**: (1) 215 mm, (2) 196 mm, (3) 121-171 mm, (4) 109 mm; 13) **minimum tail length**: (1) 181-193 mm, (2) 105-152 mm; 14) **maximum tail length**: (1) 234 mm, (2) 210 mm, (3) 187-188 mm, (4) 115-164 mm; 15) **mean tarsus length**: (1) 77 mm, (2) 50 mm, (3) 30-43 mm; 16) **wing/tail ratio**: (1) 75 mm, (2) 58-71 mm, (3) 52-54 mm; 17) **wing/tarsus ratio**: (1) 22 mm, (2) 18-19 mm, (3) 12-16 mm; 18) **tail/tarsus ratio**: (1) 36 mm, (2) 29-31 mm, (3) 21-27 mm; 19) **breast**: (1) heavily streaked or barred, (2) lightly streaked or barred, (3) clear breast, (4) complex; 20) **back**: (1) streaked, (2) barred, (3) clear; 21) **wings**: (1) red, (2) blue; 22) **tail color**: (1) red or brown, (2) blue; 23) **tail barring**: (1) multi-banded, (2) single band, (3) no band, (4) complex; 24) **malar**: (1) none, (2) 1 present, (3) 2 present; 25) **head color**: (1) uniform, (2) variable; 26) **foot color**: (1) yellow, (2) red.

Taxa	Characters																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
<i>F. tinnunculus</i>	1	2	2	2	1	1	1	1	2	2	2	3	2	3	3	2	3	3	1	1	1	2	2	2	2	1
<i>F. moluccensis</i>	1	2	2	2	1	1	1	1	2	2	2	?	?	?	3	?	2	?	1	2	1	2	1	2	1	1
<i>F. cenchroides</i>	1	3	2	2	1	1	3	1	2	2	2	3	?	?	3	2	3	3	2	1	1	2	2	2	1	1
<i>F. sparverius</i>	1	3	3	3	1	1	1	1	3	2	2	3	2	4	3	2	2	2	4	2	1	1	4	3	2	1
<i>F. newtoni</i>	1	2	1	2	3	1	3	1	3	2	2	3	2	4	3	2	2	2	4	1	1	2	1	2	2	1
<i>F. punctatus</i>	3	3	1	1	3	1	1	1	3	2	2	3	2	4	3	1	1	2	1	2	1	1	1	1	1	1
<i>F. araea</i>	3	2	1	2	2	1	2	1	3	3	2	4	2	4	3	2	1	2	3	2	1	2	1	2	1	1
<i>F. naumanni</i>	1	1	3	2	2	1	3	1	2	2	2	3	2	4	3	2	3	3	1	2	1	1	1	2	1	1
<i>F. alopez</i>	3	1	1	1	1	1	1	1	2	2	2	2	1	2	3	2	3	3	2	1	1	1	1	1	1	1
<i>F. rupicoloides</i>	1	1	1	2	1	2	3	1	2	2	2	3	2	3	2	2	2	2	1	2	1	2	1	1	1	1
<i>F. ardosiaceus</i>	1	3	1	1	3	1	2	2	2	2	2	3	2	4	3	2	2	3	2	1	2	2	3	1	1	1
<i>F. dickinsoni</i>	1	3	1	1	2	1	1	2	2	2	2	3	2	4	3	2	3	3	2	3	2	2	1	1	1	1
<i>F. zoniventris</i>	2	2	1	1	2	1	3	2	2	2	2	3	2	4	3	2	3	3	1	2	2	2	1	1	1	1
<i>F. vespertinus</i>	1	1	3	2	2	1	1	3	2	2	2	3	2	4	3	3	3	3	1	2	2	2	1	2	2	2
<i>F. amurensis</i>	1	1	3	2	2	1	1	3	2	2	2	3	2	4	3	3	3	3	1	1	2	2	1	2	1	2
<i>B. buteo</i>	2	1	1	4	3	2	3	3	1	1	1	1	1	1	1	3	2	1	1	3	1	1	1	1	1	1

Table 5: Character-state data for male kestrels in the genus *Falco* plus the outgroup (*B. buteo*). Character (character-state) key: 1) **Hovering**: (1) yes, (2) rarely, (3) no; 2) **wing size dimorphism**: (1) 3%, (2) 3.1-6.0%, (3) 6.1 + %; 3) **color dimorphism**: (1) uniform, (2) tail different, (3) bicolored; 4) **plumage change from juvenal to adult**: (1) no change, (2) male changes, (3) juvenal resembles male, (4) both sexes change; 5) **overall color**: (1 - 5) uniform to multicolored; 6) **eye color**: (1) dark, (2) pale; 7) **juvenal streaked**: (1) streaked, (2) solid, (3) variable; 8) **color**: (1) red, (2) gray, (3) red & gray; 9) **mean wing length**: (1) 387 mm, (2) 276-280 mm, (3) 216-246 mm, (4) 148-187 mm; 10) **minimum wing length**: (1) 368 mm, (2) 205-266 mm, (3) 146-180 mm; 11) **maximum wing length**: (1) 404 mm, (2) 290-293, (3) 182-260 mm, (4) 151 mm; 12) **mean tail length**: (1) 196-208 mm, (2) 162 mm, (3) 120-147 mm, (4) 107 mm; 13) **minimum tail length**: (1) 194 mm, (2) 180 mm, (3) 105-150 mm; 14) **maximum tail length**: (1) 212-223 mm, (2) 174-187 mm, (3) 130-155 mm, (4) 110 mm; 15) **mean tarsus length**: (1) 75 mm, (2) 50 mm, (3) 28-43 mm; 16) **wing/tail ratio**: (1) 70-76 mm, (2) 59-66 mm, (3) 52-54 mm; 17) **wing/tarsus ratio**: (1) 23-24 mm, (2) 21 mm, (3) 15-19 mm, (4) 12-13 mm; 18) **tail/tarsus ratio**: (1) 36 mm, (2) 29-32 mm, (3) 25-26 mm, (4) 22-23 mm; 19) **breast**: (1) heavily streaked or barred, (2) lightly streaked or barred, (3) clear breast, (4) complex; 20) **back**: (1) streaked, (2) barred, (3) clear; 21) **wings**: (1) red, (2) blue; 22) **tail color**: (1) red or brown, (2) blue; 23) **tail barring**: (1) multi-banded, (2) single band, (3) no band; 24) **malar**: (1) none, (2) 1 present, (3) 2 present; 25) **head color**: (1) uniform, (2) variable; 26) **foot color**: (1) yellow, (2) red.

Taxa	Characters																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
<i>F. tinnunculus</i>	1	2	2	2	5	1	3	1	2	3	2	3	2	3	3	3	2	3	1	1	1	2	2	2	2	1
<i>F. moluccensis</i>	1	2	2	2	5	1	1	1	3	?	?	3	2	3	2	3	2	3	1	2	1	2	1	2	1	1
<i>F. cenchroides</i>	1	3	2	2	5	1	3	1	3	?	?	3	2	4	3	3	2	3	2	1	1	2	2	2	1	1
<i>F. sparverius</i>	1	3	3	3	4	1	3	1	3	3	3	3	1	2	2	4	3	3	4	2	2	1	2	3	2	1
<i>F. newtoni</i>	1	2	1	2	4	1	3	1	3	3	3	3	2	3	2	4	3	3	1	1	2	1	2	2	1	
<i>F. punctatus</i>	3	3	1	1	4	1	1	1	3	3	3	3	1	1	2	4	3	3	1	2	1	1	1	1	1	1
<i>F. araea</i>	3	2	1	2	4	1	2	1	4	3	4	4	1	1	2	4	3	4	3	2	1	2	1	2	1	1
<i>F. naumanni</i>	1	1	3	2	2	1	1	1	3	3	3	3	2	4	4	3	2	3	2	3	2	2	2	1	1	1
<i>F. alopex</i>	3	1	1	1	1	1	1	1	1	2	1	3	1	3	4	2	2	2	2	1	1	1	1	1	1	1
<i>F. rupicoloides</i>	1	1	1	2	1	2	3	1	2	3	2	2	2	3	2	2	2	2	1	2	1	2	1	1	1	1
<i>F. ardosiaceus</i>	1	3	1	1	4	1	2	2	3	3	3	3	2	3	2	3	2	3	2	1	2	2	3	1	1	1
<i>F. dickinsoni</i>	1	3	1	1	4	1	1	2	3	3	3	3	2	3	3	3	2	3	2	3	2	2	1	1	1	1
<i>F. zoniventris</i>	2	2	1	1	2	1	3	2	3	3	3	3	2	3	3	3	2	3	1	2	2	2	1	1	1	1
<i>F. vespertinus</i>	1	1	3	2	2	1	2	3	3	3	3	3	3	4	4	3	2	3	2	3	2	2	3	1	1	2
<i>F. amurensis</i>	1	1	3	2	2	1	2	3	3	3	3	3	3	4	4	3	1	3	2	3	2	2	3	1	1	2
<i>F. buteo</i>	2	1	1	4	3	2	3	3	1	1	1	1	3	3	1	1	2	1	1	3	1	1	1	1	1	1

Table 6: Character-state data for female kestrels in the genus *Falco* plus the outgroup (*B. platypterus*). Character (character-state) key: 1) **Hovering**: (1) yes, (2) rarely, (3) no; 2) **wing size dimorphism**: (1) 3%, (2) 3.1-6.0%, (3) 6.1 + %; 3) **color dimorphism**: (1) uniform, (2) tail different, (3) bicolored; 4) **plumage change from juvenal to adult**: (1) no change, (2) male changes, (3) juvenal resembles male, (4) both sexes change; 5) **overall color**: (1 - 3) uniform to multicolored; 6) **eye color**: (1) dark, (2) pale; 7) **juvenal streaked**: (1) streaked, (2) solid, (3) variable; 8) **color**: (1) red, (2) gray, (3) red & gray; 9) **mean wing length**: (1) 223-398 mm, (2) 154-195 mm; 10) **minimum wing length**: (1) 255-274 mm, (2) 210-235 mm, (3) 178-188 mm, (4) 152 mm; 11) **maximum wing length**: (1) 234-419 mm, (2) 186-207 mm, (3) 156 mm; 12) **mean tail length**: (1) 196-215 mm, (2) 121-171 mm, (3) 109 mm; 13) **minimum tail length**: (1) 181-193 mm, (2) 111-152 mm, (3) 105 mm; 14) **maximum tail length**: (1) 210-234 mm, (2) 187-188 mm, (3) 131-164 mm, (4) 115 mm; 15) **mean tarsus length**: (1) 77 mm, (2) 50 mm, (3) 28-43 mm; 16) **wing/tail ratio**: (1) 75 mm, (2) 71 mm, (3) 58-68 mm, (4) 52-53; 17) **wing/tarsus ratio**: (1) 22 mm, (2) 18-19 mm, (3) 29-31 mm; 18) **tail/tarsus ratio**: (1) 36 mm, (2) 29-31 mm, (3) 21-27 mm; 19) **breast**: (1) heavily streaked or barred, (2) lightly streaked or barred, (3) clear breast, (4) complex; 20) **back**: (1) streaked, (2) barred, (3) clear; 21) **wings**: (1) red, (2) blue; 22) **tail color**: (1) red or brown, (2) blue; 23) **tail barring**: (1) multi-banded, (2) single band, (3) no band, (4) complex; 24) **malar**: (1) none, (2) 1 present, (3) 2 present; 25) **head color**: (1) uniform, (2) variable; 26) **foot color**: (1) yellow, (2) red.

Taxa	Characters																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
<i>F. tinnunculus</i>	1	2	2	2	1	1	1	1	1	2	1	2	2	2	3	3	3	3	1	2	1	1	1	2	1	1
<i>F. moluccensis</i>	1	2	2	2	1	1	1	1	1	2	1	?	?	?	3	?	2	?	1	2	1	2	1	2	1	1
<i>F. cenchroides</i>	1	3	2	2	1	1	3	1	1	1	1	2	?	?	3	3	3	3	2	1	1	2	2	2	1	1
<i>F. sparverius</i>	1	3	3	3	3	1	1	1	2	3	2	2	2	3	3	3	2	2	4	2	1	1	4	3	2	1
<i>F. newtoni</i>	1	2	1	2	3	1	3	1	2	3	2	2	2	3	3	3	2	2	4	1	1	2	1	2	2	1
<i>F. punctatus</i>	3	3	1	1	3	1	1	1	2	3	2	2	?	?	3	1	1	2	1	2	1	1	1	1	1	1
<i>F. araea</i>	3	2	1	2	2	1	2	1	2	4	3	3	3	4	3	2	1	2	3	2	1	2	1	2	1	1
<i>F. naumanni</i>	1	1	3	2	2	1	3	1	1	2	1	2	2	3	3	3	3	3	1	2	1	1	1	2	1	1
<i>F. alopex</i>	3	1	1	1	1	1	1	1	1	1	1	1	1	1	3	3	3	3	2	1	1	1	1	1	1	1
<i>F. rupicoloides</i>	1	1	1	2	1	2	3	1	1	1	1	2	2	2	2	3	2	2	1	2	1	2	1	1	1	1
<i>F. ardosiaceus</i>	1	3	1	1	3	1	2	2	1	2	1	2	2	3	3	3	2	3	2	1	2	2	3	1	1	1
<i>F. dickinsoni</i>	1	3	1	1	2	1	1	2	1	2	1	2	2	3	3	3	3	3	2	3	2	2	1	1	1	1
<i>F. zoniventris</i>	2	2	1	1	2	1	3	2	1	2	1	2	2	3	3	3	3	3	1	2	2	2	1	1	1	1
<i>F. vespertinus</i>	1	1	3	2	2	1	1	3	1	2	1	2	2	3	3	4	3	3	1	2	2	2	1	2	2	2
<i>F. amurensis</i>	1	1	3	2	2	1	1	3	1	2	1	2	2	3	3	4	3	3	1	1	2	2	1	2	1	2
<i>B. platypterus</i>	3	3	1	4	2	2	3	2	1	1	1	2	2	2	1	3	1	1	1	3	1	1	1	1	1	1

Table 7: Character-state data for male kestrels in the genus *Falco* plus the outgroup (*B. platypterus*). Character (character-state) key: 1) **Hovering**: (1) yes, (2) rarely, (3) no; 2) **wing size dimorphism**: (1) 3%, (2) 3.1-6.0%, (3) 6.1 + %; 3) **color dimorphism**: (1) uniform, (2) tail different, (3) bicolored; 4) **plumage change from juvenal to adult**: (1) no change, (2) male changes, (3) juvenal resembles male, (4) both sexes change; 5) **overall color**: (1 - 5) uniform to multicolored; 6) **eye color**: (1) dark, (2) pale; 7) **juvenal streaked**: (1) streaked, (2) solid, (3) variable; 8) **color**: (1) red, (2) gray, (3) red & gray; 9) **mean wing length**: (1) 286-387 mm, (2) 216-246 mm, (3) 148-187 mm; 10) **minimum wing length**: (1) 205-368 mm, (2) 146-180 mm; 11) **maximum wing length**: (1) 223-404 mm, (2) 182-198 mm, (3) 151 mm; 12) **mean tail length**: (1) 196-208 mm, (2) 162 mm, (3) 120-147 mm, (4) 107 mm; 13) **minimum tail length**: (1) 180-194 mm, (2) 105-150 mm; 14) **maximum tail length**: (1) 212-223 mm, (2) 187 mm, (3) 174 mm, (4) 131-164 mm, (5) 110 mm; 15) **mean tarsus length**: (1) 75 mm, (2) 50 mm, (3) 28-43 mm; 16) **wing/tail ratio**: (1) 76 mm, (2) 73 mm, (3) 70 mm, (4) 63-66 mm, (5) 54-60 mm, (6) 52-53 mm; 17) **wing/tarsus ratio**: (1) 23-24 mm, (2) 21 mm, (3) 15-19 mm, (4) 12-13 mm; 18) **tail/tarsus ratio**: (1) 36 mm, (2) 29-32 mm, (3) 25-26 mm, (4) 22-23 mm; 19) **breast**: (1) heavily streaked or barred, (2) lightly streaked or barred, (3) clear breast, (4) complex; 20) **back**: (1) streaked, (2) barred, (3) clear; 21) **wings**: (1) red, (2) blue; 22) **tail color**: (1) red or brown, (2) blue; 23) **tail barring**: (1) multi-banded, (2) single band, (3) no band, (4) complex; 24) **malar**: (1) none, (2) 1 present, (3) 2 present; 25) **head color**: (1) uniform, (2) variable; 26) **foot color**: (1) yellow, (2) red.

Taxa	Characters																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
<i>F. tinnunculus</i>	1	2	2	2	5	1	3	1	2	1	1	2	2	3	3	4	3	3	1	1	1	2	2	2	2	1
<i>F. moluccensis</i>	1	2	2	2	5	1	1	1	2	1	1	3	?	?	3	4	3	2	1	2	1	2	1	2	1	1
<i>F. cenchroides</i>	1	3	2	2	5	1	3	1	2	1	1	3	?	?	3	5	4	3	2	1	1	2	2	2	1	1
<i>F. sparverius</i>	1	3	3	3	4	1	3	1	3	2	2	3	2	4	3	3	2	2	4	2	2	1	2	3	2	1
<i>F. newtoni</i>	1	2	1	2	4	1	3	1	3	2	2	3	2	4	3	4	3	2	1	1	1	2	1	2	2	1
<i>F. punctatus</i>	3	3	1	1	4	1	1	1	3	2	2	3	2	4	3	1	1	2	1	2	1	1	1	1	1	1
<i>F. araea</i>	3	2	1	2	4	1	2	1	3	2	3	4	2	5	3	2	1	2	3	2	1	2	1	2	1	1
<i>F. naumanni</i>	1	1	3	2	2	1	1	1	2	1	1	3	2	4	3	5	4	4	2	3	2	2	2	1	1	1
<i>F. alopex</i>	3	3	1	1	1	1	1	1	1	1	1	1	1	1	1	3	3	3	2	1	1	1	1	1	1	1
<i>F. rupicoloides</i>	1	1	1	2	1	2	3	1	1	1	1	2	2	2	2	5	3	2	1	2	1	2	1	1	1	1
<i>F. ardosiaceus</i>	1	3	1	1	4	1	2	2	2	1	1	3	2	4	3	4	3	2	2	1	2	2	3	1	1	1
<i>F. dickinsoni</i>	1	3	1	1	4	1	1	2	2	1	1	3	2	4	3	4	3	3	2	3	2	2	1	1	1	1
<i>F. zoniventris</i>	2	2	1	1	2	1	3	2	2	1	1	3	2	4	3	4	3	3	1	2	2	2	1	1	1	1
<i>F. vespertinus</i>	1	1	3	2	2	1	2	3	2	1	1	3	2	4	3	6	4	4	2	3	2	2	3	1	1	2
<i>F. amurensis</i>	1	1	3	2	2	1	2	3	2	1	1	3	2	4	3	6	4	4	2	3	2	2	3	1	1	2
<i>B. platypterus</i>	3	3	1	4	2	2	3	2	1	1	1	2	2	3	1	5	1	1	1	3	1	1	1	1	1	1

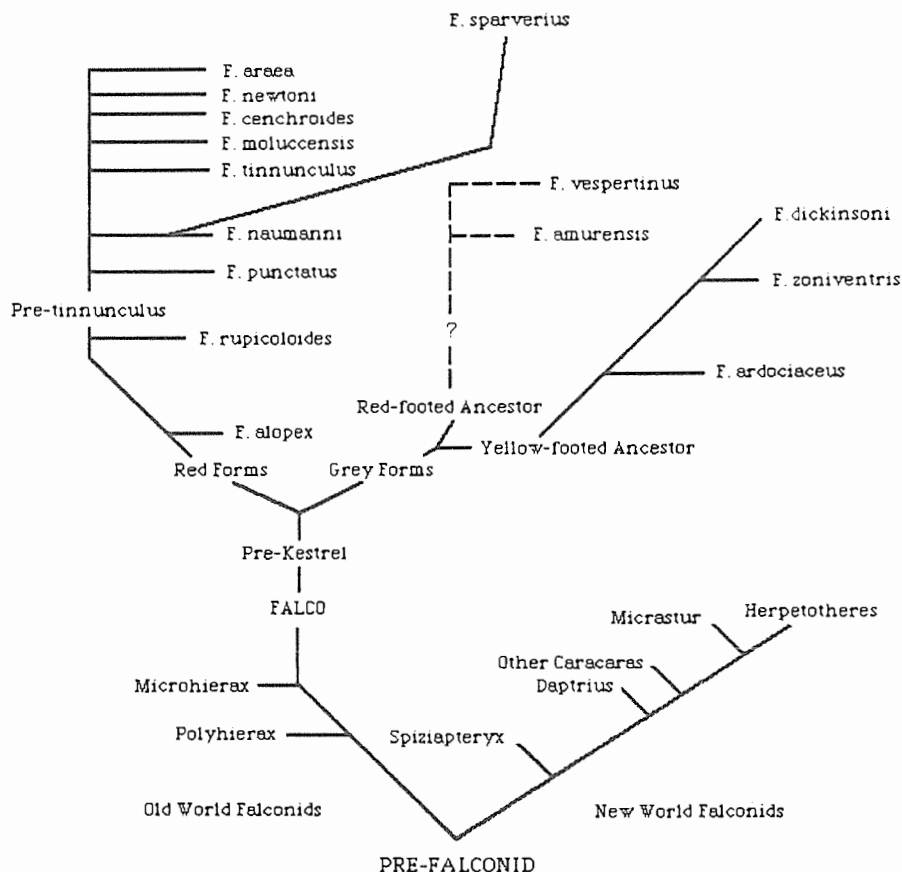


Figure 1: Our hypothetical phylogeny of kestrels prior to using cladistic techniques to derive figures 2-5. Note the heavy emphasis on red forms and gray forms and on the red-footed forms and yellow-footed forms in the construction of the "tinnunculus-like" kestrels.

alopez) as the F0G (oldest member of the kestrels). The fourth T1G T0G (G2) analysis listed the Greater Kestrel (*F. rupicoloides*) as more closely related to the T0G than *F. alopex*, but *F. alopex* was placed as the second oldest member of the clade. We used each as a F0G to see if the F1G cladograms were different; they were identical. We consider *F. alopex* to be the oldest member of the kestrel clade.

Our intuitive systematic arrangement of kestrels, considering both sexes and based on the data in Tables 1-3, is shown in Fig. 1. We constructed this figure prior to analyzing the data cladistically. Our cladistic results (Figs. 2-5) varied somewhat from our intuitive impression. For example, we had envisioned red forms and gray forms separating from a common hypothetical ancestor. The cladograms (Figs. 2-5) show, however, *F. alopex* as being ancestral to the 2 color morphs. Our grouping of the gray forms into 2 separate clades was substantiated. The *F. vespertinus* and *F. amurensis* clade, however, had *F. naumanni* associated with it in 3 groups (G1-G3). In Fig. 1 we were unable to envision the correct relationship among the remaining kestrels. The

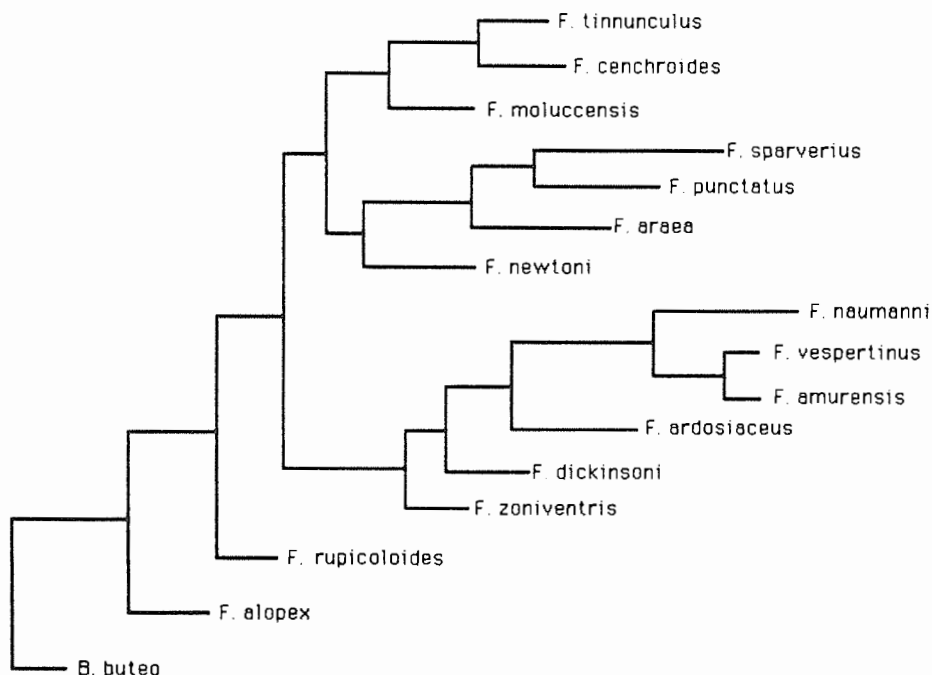


Figure 2: Phylogenetic relationships of 15 species of male kestrels in the genus *Falco*. The tree is rooted to *Buteo buteo*. An analysis of 26 unordered characters produced a best-fit tree of 84 steps ($CI = 0.58$).

cladograms (Figs. 2-5) all placed *F. sparverius*, *F. punctatus* (Mauritius Kestrel), *F. araea*, and *F. newtoni* (Madagascar Kestrel) into a single clade. Three species, *F. moluccensis* (Moluccean Kestrel), *F. tinnunculus* and *F. cenchroides* (Australian Kestrel), consistently showed close affinity and formed another clade.

Male cladograms (Figs. 2 and 3) differ in pattern, in a number of respects, depending on the TOG used. First, the placement of the *F. vespertinus*/*F. amurensis*/*F. naumanni* (VAN) clade relative to the *F. zoniventris*/*F. ardosiaceus*/*F. dickinsoni* (ZAD) clade was very different. In the *B. buteo* root, the VAN clade is younger and derived from the ZAD clade. In the *B. platypterus* root, the VAN clade is older and of separate derivation. The female cladograms support 1) the ZAD clade as being older and 2) the VAN group as not being directly descended from the ZAD group. The most parsimonious arrangement then would place the ZAD group as older and the VAN group as derived from a hypothetical sister to the ZAD clade. The *F. tinnunculus*/*F. cenchroides*/*F. moluccensis* (TCM) clade is in agreement between both phylogenies. The juxtaposition of the *F. sparverius*/*F. punctatus*/*F. araea*/*F. newtoni* (SPAN) clade is in agreement on age but not on sister species arrangement. The female phylogenies support the *F. sparverius*/*F. newtoni* sister species grouping.

The phylogenies (Figs. 4 and 5) for females were very different. The most apparent conflict is with the placement of *F. cenchroides*. In the *B. buteo* rooted tree *F. cenchroides* groups with the TCM clade. In the *B. platypterus* rooting *F. cenchroides* is placed between *F. alopex* and *F. rupicoloides* (i.e., very old). The most parsimonious placement,

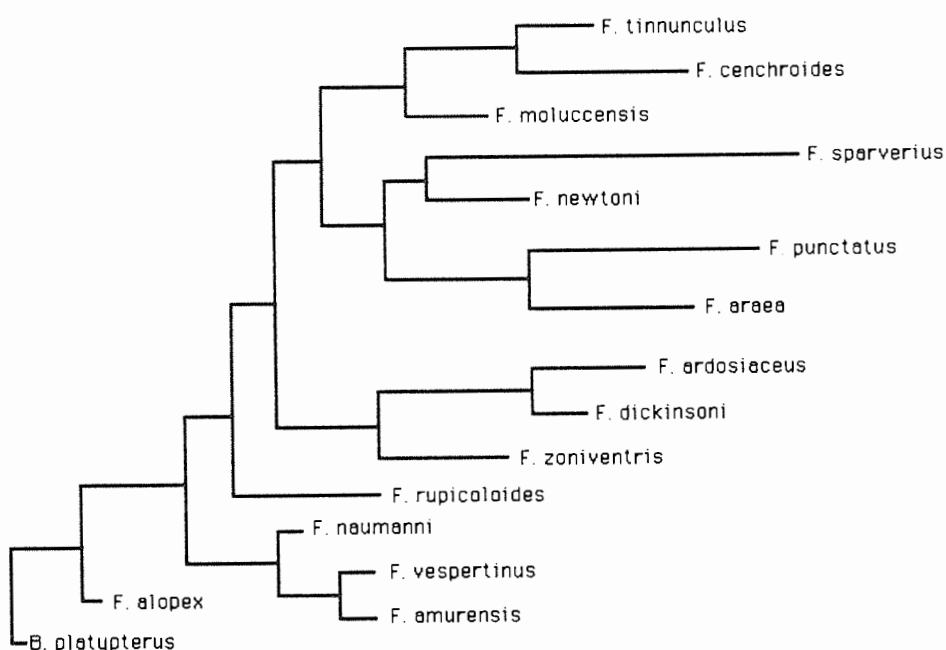


Figure 3: Phylogenetic relationships of 15 species of male kestrels in the genus *Falco*. The tree is rooted to *Buteo platypterus*. An analysis of 26 unordered characters produced a best-fit tree of 88 steps ($C1 = 0.60$).

when considering male phylogenies, is with the TCM clade. The SPAN clade is in general agreement. *Falco sparverius* and *F. newtoni* are considered sister species. The VAN and ZAD clades are well defined except for age. In the *B. buteo* tree VAN is younger and in the *B. platypterus* tree it is the same relative age as the ZAD clade.

We believe the most parsimonious relationship among all groups (i.e., among both male and female trees) is one similar to the tree shown in Fig. 2. The VAN-ZAD clade conflict does not involve an age component as the VAN clade is much younger. In question is just how they are related to each other. The 2 plausible scenarios are 1) VAN is derived from ZAD or 2) VAN and ZAD are sister clades sharing a common hypothetical ancestor. The VAN/ZAD clades together form a larger clade whose sister clade is the TCM/SPAN group. Finally, we believe *F. sparverius* to be the most recently evolved member in the kestrel group.

DISCUSSION

Types of Kestrels

There are generally 2 color types in the adult plumage, among species considered to be kestrels; there are gray forms and red forms. The gray forms are Dickinson's Kestrel, Grey Kestrel, and Madagascar Banded Kestrel. Additionally in the adult male plumage there are the grey Red-footed Falcons. The red forms include, for example, such divergent species as the Fox Kestrel, Mauritius Kestrel, and the Eurasian Kestrel

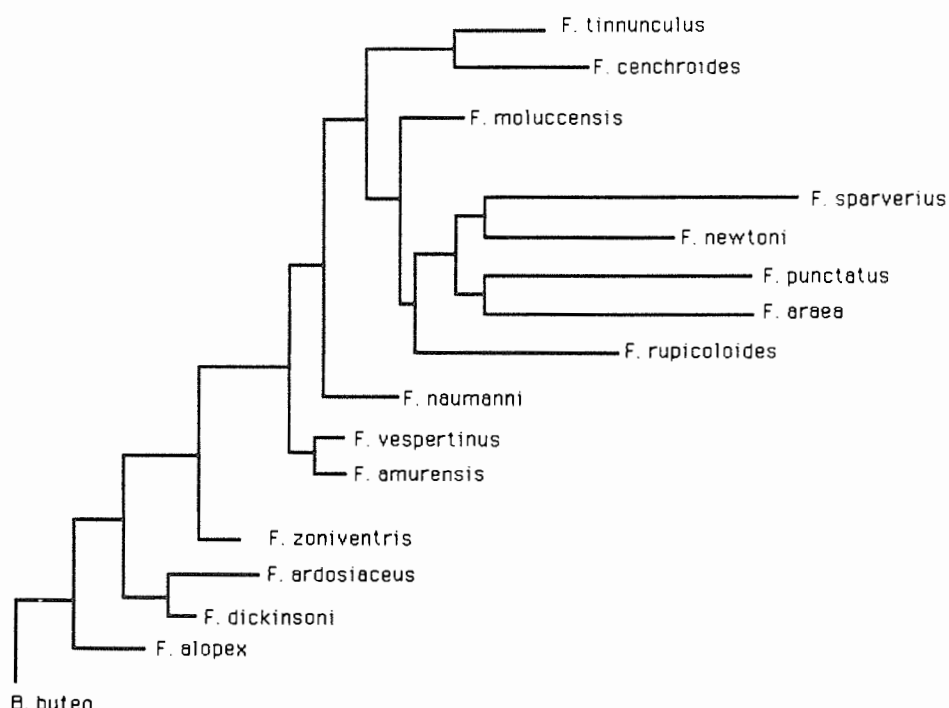


Figure 4: Phylogenetic relationships of 15 species of female kestrels in the genus *Falco*. The tree is rooted to *Buteo buteo*. An analysis of 26 unordered characters produced a best-fit tree of 74 steps ($CI = 0.57$).

type. It appears that the primitive red form of *F. alopex* was the ancestor of the current red and gray kestrel types.

Juveniles of most species usually differ from adults in having a more “generalized” and in this case primitive plumage (i.e., uniformly colored with dark ventral streaks and dark tail bars, Table 1). These can be quickly compared by looking at plates 35 and 36 in Weick (1980).

Phylogeny

We believe ancestral falconids or perhaps even pre-*Falco* occurred in at least two generalized habitat types. We suggest that those in forested regions tended to take on a dark (gray or black) bicolored appearance, perhaps with some barring, as seen in the falconets (*Microhierax*), in *Herpetotheres*, *Micrastur* and some forest caracaras (*Daptrius*). *Micrastur ruficollis* has in fact, both a red and a gray color form. Ancestral stocks living in open country were possibly uniformly colored (browns or reds) with streaking as seen in many open land (grassland and savannah) bird species today.

The colored, streaked plumage pattern in falconids is probably an “ancestral” rather than derived trait (Table 1). Such a plumage pattern is found characteristically in juvenile plumages throughout many bird groups related to *Falco* such as *Buteo* and *Accipiter* (out-groups) and in many more distantly related groups such as waterfowl, bitterns,

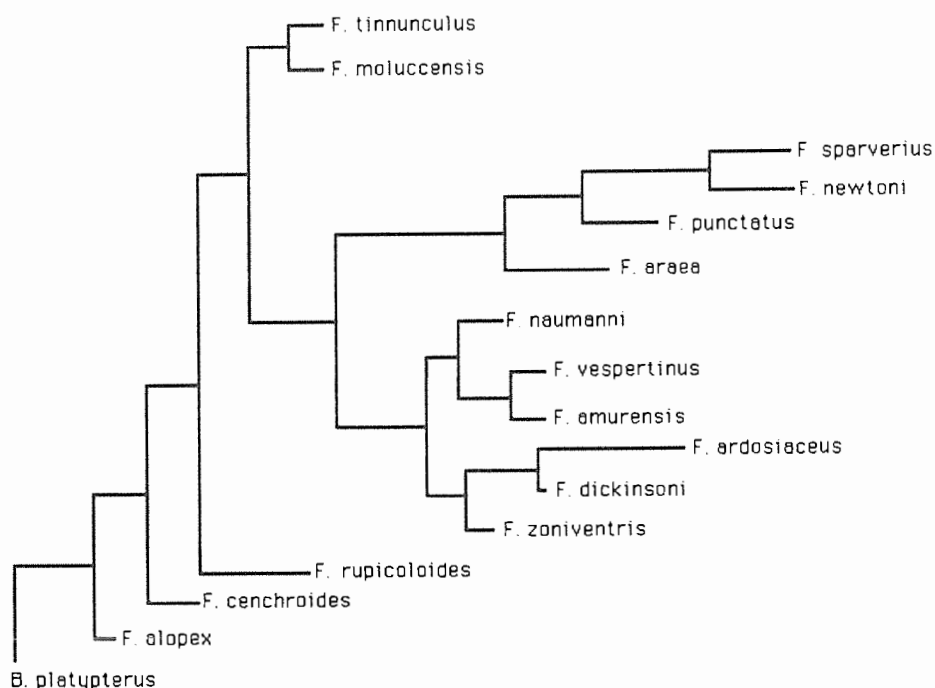


Figure 5: Phylogenetic relationships of 15 species of female kestrels in the genus *Falco*. The tree is rooted to *Buteo platypterus*. An analysis of 26 unordered characters produced a best-fit tree of 82 steps (C1 = 0.60).

and passerines. It is found in juvenal plumages of open country caracaras (*Milvago*, *Phalcoboenus*) and most *Falco*. We agree with Vaurie (1961) that juvenal plumage tends to be conservative and thus the ancestral plumage condition. Departures from it are thus derived. For example, color patterns frequently seen in adult males are derived secondary sex traits for breeding. Ancestral *Falco* in Africa could have had the 2 color types, a dark (gray) and a brown or red form as seen in contemporary *Micrastur*. While pure speculation, one may evoke such an idea to explain both red and gray kestrels in Africa.

The Gray Kestrels. – We propose a single phylogeny for the gray kestrel group that split at an early period (Figs. 2-5). We suggest that at least the 3 Ethiopian Realm (one in Madagascar) species are older than most of the contemporary red or brown species. They show little age color dimorphism and the juvenal plumage has a decidedly streaked appearance. The species on Madagascar (*F. zoniventris*) appears to be the oldest of the group. *F. dickinsoni* and *F. ardosiaceus* are sister species as suggested by distribution, color pattern and structural features.

Gray-colored kestrels are easily subdivided into 2 groups; those with red feet and considerable sexual color dimorphism (Eurasian breeders) and those with yellow feet and little or no sexual color dimorphism (African and Madagascar breeders). In the red-footed group, *F. vesperinus* may be unique among *Falco* in having a distinctive male plumage (immature) that comes between juvenile and adult plumages. Because of the degree of color dimorphism, any sort of numerical rating system based on the increasing

complexity of color pattern would rate them high. We recognize that *F. amurensis* and *F. vespertinus* are distinct in several ways, but we have chosen to treat them in the manner we have until other biochemical, morphological or behavioral traits are available to define their relationship more clearly. Currently unpublished DNA-DNA hybridization data (J. Ahlquist pers. comm.) on such divergent falcon species as *F. vespertinus*, *F. sparverius*, *F. novaezeelandiae*, *F. rupicoloides* and *F. berigora* fail to present any clear solution to the problem.

Because Red-footed Falcons depart further from the general kestrel form than do other kestrels, Cade (1982) places them with hobbies. While not totally convincing, there are some reasons for our suggestion that Red-footed Falcons may be derived from an African ancestor. First, besides being gray as adults, they return to Africa seasonally on a long migration to winter in the same range as the African gray forms. *F. amurensis*, makes an extremely long, and perhaps over water, flight from eastern Asia to arrive in Africa. In contrast, other raptors from far Eastern Siberia and China migrate south into Southeast Asia instead of taking the long diagonal course to Africa. They typically migrate in the company of Lesser Kestrels (Brown 1976), which also pass their winter season in Africa. In the cladograms *F. naumanni* shares a direct hypothetical ancestor to *F. amurensis* and *F. vespertinus*.

The Red Forms. - The relationships among red forms is fairly certain, but the juxtaposition within subclades TCM and SPAN is variable. *F. alopec* is the oldest form followed by *F. rupicoloides*, *F. moluccensis*, *F. newtoni*, *F. tinnunculus*, *F. cenchroides*, *F. araea*, *F. punctatus*, and finally *F. sparverius*. The Fox Kestrel is most primitive because 1) it does not hover and 2) there is essentially no age or sex color dimorphism (both of which we consider derived [Vaurie 1961]). Therefore, kestrels with no color dimorphism are closer to the ancestral type and primitive condition. Among the island forms, most derived is *F. punctatus* of the Mauritius Islands. It probably has the least quantifiable age-related color dimorphism of any *Falco*. In both age and sex categories the plumage is quite like a female *F. tinnunculus* type. It has certainly been isolated in forested habitat long enough to acquire a more rounded, *Accipiter*-like wing and overall accipiterine shape than any other *Falco* except perhaps *F. novaezeelandiae*. It also does not hover. *F. punctatus* likely speciated from an early *F. tinnunculus* or proto-*F. newtoni* stock that had previously invaded the islands. The lack of sexual color dimorphism may represent either the ancestral condition or the secondary loss of dimorphism, a common occurrence in island birds. This is especially true if populations are small, the island lacks a congener, the island is isolated from further invasions, and the founding propogule had certain traits by chance. Cade (1982) reckoned that in the best of times, under pristine conditions, the total *F. punctatus* population only numbered a few hundred individuals. Its modifications should not be surprising.

We consider the Greater Kestrel to be close in plumage to the ancestral type since it also lacks any conspicuous sexual color dimorphism and is therefore, older than most other red forms. However, the white iris, rather than brown, is probably a secondarily derived rather than primitive trait. The white iris may have developed to help isolate it from more recently invading, similar looking kestrels (i.e., *F. tinnunculus*). However, in the case of *F. alopec* and *F. rupicoloides*, one might attempt to argue that their form is highly derived. This would account for their departure from the general kestrel trend (see Brown et al. 1982). Our cladistic analysis however, shows them to be more closely related to the primitive outgroup than any of the other kestrels. They are not highly derived.

An ancestor to the TCM clade (4 *F. tinnunculus*-like species) apparently radiated to form a superspecies (Stresemann and Amadon 1979) or species group (Snow 1978).

F. moluccensis evolved early while *F. cenchroides* speciated relatively recently. A first invasion into Southeast Asia and subsequent speciation would account for *F. moluccensis* and a second more recent invasion, moving over *F. moluccensis* and going into Australia, would account for *F. cenchroides*. This hypothesis would correlate nicely with Plio-Pleistocene glacial phenomena that forced species out of northern regions and into southern areas.

The island species, *F. newtoni* and *F. araea* probably evolved in a similar fashion (Fig. 1). That is, an invading TCM ancestor became isolated on individual islands and speciated. *F. araea* is probably a more recent invader than is *F. newtoni* based also on plumage characteristics. *F. sparverius* has also been included with the above species as a part of the species group. *F. moluccensis* in particular, and probably *F. cenchroides*, *F. araea* and perhaps *F. newtoni* clearly form such a superspecies with *F. tinnunculus*, but we are uncertain that *F. sparverius* does.

F. sparverius appears to be the most recently evolved species of kestrel. It departs significantly from the primitive form in sexual color dimorphism and it is the only species in the genus with juvenal plumages of each sex resembling their respective adult sex rather than just the female. We consider sex-age plumage similarity to be a derived condition (see Table 1). Also *F. sparverius* occupies an extensive range (Alaska to Tierra del Fuego in South America) with 14 recognized races, yet none of the isolated races has diverged enough to obtain species status.

F. sparverius is the only kestrel known to have colonized North and South America. The American Kestrel may be related to *F. naumanni* because only these 2 species have blue secondary feathers and greater wing coverts in the males. Juvenal male *F. naumanni* also frequently tend toward adult males in color rather than the female. The Lesser Kestrel is a colonial falcon and could have provided the original American stock by being blown over as a migrating group. Recall that the Cattle Egret (*Ardeola ibis*) recently invaded South America probably from Africa and then moved north into North America. The other logical pathway for pre-*sparverius* stock to have reached North America is across the Bering Sea region.

Areas of Interpretive Concern

Our first assumption is that gray forms are kestrels. If not, our argument that Africa is the site of kestrel origin is weakened. Some evidence exists contradicting our contention that gray-colored kestrels are indeed kestrels (*sensus stricto*). First, they rarely hover. Second, the beak of *F. ardosiaceus* is far more massive than other kestrels—even than those of greater size such as *F. tinnunculus* and *F. rupicoloides*. These could be derived traits however, for feeding, correlated with the frequently occurring double tooth on the upper mandible. Third, *F. zoniventris* is primarily a forest species rather than a savannah type (this, of course, could be derived as a function of food habits as *F. punctatus* is also a forest inhabitant). *F. zoniventris* is also very unkestrel-like as it does not have head-bobbing movements (Laugrand and Meyburg 1984). Lastly, *F. dickinsoni* is quite unkestrel-like in some of its behavior (A. Kemp pers. comm.), and bill and foot structure, but these too could be derived conditions because of the habitat it occupies (see Brown et al. 1982).

The second assumption is that *F. alopec* was derived or speciated *in situ* in Africa from an early kestrel or a pre-kestrel type. If not, it must have been an early immigrant from the Palearctic or simply an ancient isolate. Along with this is the assumption that it is a primitive form similar to ancestral kestrels rather than having derived traits. This last assumption appears to be correct.



Figure 6: The breeding locations of 15 species of kestrels. 1 = *F. alopec*, 2 = *F. rupicoloides*, 3 = *F. zoniventris*, 4 = *F. dickinsoni*, 5 = *F. ardosiaceus*, 6 = *F. naumanni*, 7 = *F. vespertinus*, 8 = *F. amurensis*, 9 = *F. newtoni*, 10 = *F. moluccensis*, 11 = *F. tinnunculus*, 12 = *F. cenchroides*, 13 = *F. araea*, 14 = *F. punctatus*, 15 = *F. sparverius*.

Lastly, the relationship of position of the red-footed forms remains to be clarified. We suspect biochemical analyses will provide the major breakthrough on this question.

CONCLUSIONS

The breeding locations of the 15 species of kestrels recognized world-wide are shown in Fig. 6.

In Africa 2 basic forms developed from which current kestrels were derived. These were the red and gray types. The red type may have been similar to, or the precursor of, the uniformly colored (with simple darker body streaking and tail barring) *F. alopez*, which essentially lacks sex and age dimorphism. The grey type may have been similar to, or the precursor of, *F. zoniventris* or *F. ardosiaceus*, which also lacks sex and age dimorphism. *F. alopez* is completely sympatric with *F. ardosiaceus*, although the range of the latter extends farther south. Neither are reported to hover. *F. ardosiaceus* clearly evolved in Africa, probably in allopatry and perhaps from the basic stock that earlier gave rise to *F. dickinsoni*.

An ancestral red stock probably gave rise to *F. alopez* in Africa and also expanded into the northern hemisphere. Once in the northern hemisphere, pre-*F. moluccensis* forms differentiated. Glaciation events in the holarctic (probably during late Pliocene and Pleistocene) forced them to invade southern regions. Subsequent isolates occupied regions to produce such species as *F. moluccensis*, *F. cenchroides*, *F. araea* and *F. newtoni*. At a still later time *F. tinnunculus* moved into Africa to occupy that continent as a breeder.

We believe the American Kestrel is the most recently derived of the group. It currently inhabits a variety of habitat types not equalled by any other kestrel and has the greatest number of recognized races. We feel that it holds the greatest provision for future genetic novelty among kestrels.

Systematists use characters to discover relationships based on character agreement (for example see Table 2 and Figs. 2-5). Cladists use exclusively derived characters and synapomorphies to construct cladograms of phylogenetic hypotheses. The characters used to construct phylogenies are sometimes questioned because they could represent instances of convergence; color is an example. Some traits may be easily changed and therefore, may not provide a clear reflection of phylogenetic relationships. Our cladistic analyses all had consistency indexes of .58-.60, meaning that homoplasy exists in our data set. A promising technique, electrophoresis, offers us a chance to examine a character set (isozymes and allozymes) which might resolve many of our conjectural phylogenetic hypotheses that are tentatively based on phenotypic characters only. The consistency index for biochemical data sets is usually .80 or higher.

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TRENDS IN AMERICAN KESTREL COUNTS FROM THE NORTH AMERICAN BREEDING BIRD SURVEY

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Abstract: A 15-year summary of the BBS data suggests that continental numbers of American Kestrels have increased during 1966-1979. According to analyses of physiographic and state/province strata, some areas are largely responsible for the increase in the U.S. and southern Canada and that only in Illinois and Arkansas have kestrels declined. BBS data are too few in Florida to detect trends concerning *F. s. paulus*.

Surveying on special Raptor Routes, on which volunteers looked specifically for raptors while retracing their BBS route, did not significantly increase the kestrel counts, but did improve detection rates.

The breeding range of the American Kestrel (*Falco sparverius*) includes southern Canada and the United States (Brown and Amadon 1968). In this transcontinental area the Breeding Bird Survey (BBS) is conducted annually to obtain indices of the numbers of breeding birds (Bystrak 1981). This paper presents the American Kestrel data from a 15-year summary of BBS (Robbins et al. 1986), and the results of some experimental counts that were designed to determine if more kestrels could be counted using different procedures.

The population status of American Kestrels has been a concern in certain parts of its range. The species is susceptible to egg-shell thinning by organochlorine contaminants (Lincer 1975, Wiemeyer and Lincer 1987), and there is evidence that some population declines have occurred (Hackman and Henny 1971, U.S. Dept. of Interior 1976). This small falcon is commonly encountered during roadside counts such as the BBS; consequently, the American Kestrel data base is comparatively large among raptor species. Therefore, we examined the BBS data to learn how well we could estimate trends in numbers of American Kestrels.

The extent of American Kestrel population changes has been difficult to evaluate because different sources of data have led to different conclusions (Henny 1972, U.S. Department of Interior 1976, Nagy 1977). Concern and confusion about population status of the American Kestrel are reflected in the comments in the National Audubon Society Blue List (e.g., Arbib 1971, 1973, 1975, 1976, 1979). The quantity of BBS data, gathered across North America for 15 years, offers a basis for assessing the status of the American Kestrel over a large portion of its breeding range.

METHODS

All the trends we present were calculated for a 15-year summary of the BBS data (Robbins et al. 1986). Robbins and Van Velzen (1967) and Bystrak (1981) have described BBS field methods, and Geissler and Noon (1981) explained the techniques for calculating the trends. Robbins et al. (1986) summarized methods and discussion of variables associated with BBS data. Generally, the BBS includes about 2,400 transects that were randomly selected from secondary roads in the U.S and Canada. Each year, volunteers count all the birds that one observer can see or hear within 400 m of the road

at 50 stops spaced at 800 m intervals. Surveys occur in June, beginning one half hour before sunrise and lasting about 4 hours.

Robbins et al. (1986) calculated trends for the continent, for eastern (to the Mississippi River), central (to the Rocky Mountains) and western regions of the U.S., for 62 physiographic strata (Bystrak 1981), and for state/provincial jurisdictions. The trends are based on the average proportional changes for each of at least 15 routes that were surveyed in 2 or more years in each region, stratum or state/province. Increases and decreases were said to be significant when there was a 95% or greater probability that the change was real and not a result of chance sampling.

Detections of most raptor species are too infrequent to allow trend analyses for many areas. We wanted to determine if we could conveniently obtain larger counts of raptors from BBS routes without interfering with the standardized BBS procedures. Therefore, we asked BBS volunteers in 15 sample states to conduct a special Raptor Route (RR) in 1980. Upon completion of their BBS, the volunteers backtracked over their 39.2 km BBS routes, looking specifically for birds of prey. The RR differed from the BBS in the following ways: 1) RR occurred later in the morning, generally starting about 4 hours after sunrise; 2) the official BBS observer and an assistant, if any, could look for raptors; 3) raptors could be counted anywhere along the route (not just from BBS stops); and 4) no stops were designated, but observers could stop at any time to identify birds.

RESULTS

The American Kestrel usually is the most frequently detected raptor on BBS routes. For example, in 1977, 1,622 were noted on 665 routes (also see Robbins and Van Velzen 1967, 1969). The Red-tailed Hawk (*Buteo jamaicensis*) was the second most common species (1,287 on 588 routes), with these 2 common species making up more than 50% of all the BBS raptor data (excluding vultures). The numbers of American Kestrels across North America significantly increased (1968-1979), as did the numbers of the eastern region (1966-1979) and central region (1967-1979).

In 11 physiographic regions there were significant increasing trends (Fig. 1). No decreasing trends were associated with physiographic regions. The number of kestrels on BBS routes increased in the Great Lakes subregion (Minnesota, Wisconsin, Michigan, Illinois, Indiana, and Ohio) and in the northeastern U.S. (West Virginia, Virginia, Maryland, Pennsylvania, New Jersey, New York, Connecticut, Vermont, New Hampshire, Maine). By state, significant increases occurred in Oregon, Montana, Minnesota, Wisconsin, Tennessee, Ohio and Pennsylvania (Fig. 1). Significant decreases occurred in Illinois and Arkansas.

The average BBS count of American Kestrels varied considerably among states. Volunteers tallied the highest counts in Idaho (2.5 per route) and California (2.3 per route). The increasing count trends in Oregon and Montana averaged 1.6 birds per route. Around the Great Lakes, increases were associated with mean counts per route of 1.7 in Minnesota, 0.7 in Wisconsin and 0.9 in Ohio. In Tennessee, the increasing trend averaged 0.4 birds per route. The increasing 15-year trend in Pennsylvania involved less than 0.1 bird per route. Significant decreases occurred in Arkansas (0.2 bird per route) and Illinois (0.7 bird per route). In other states and provinces in which no trends were evident, the mean count of American Kestrels per route ranged from 0.1 (Rhode Island, Prince Edward Island and South Carolina) to 2.0 (Utah).

In Florida, where the subspecies *F. s. paulus* breeds, there was a mean of 0.3 bird per route. No trend could be calculated for Florida because there were fewer than 15 BBS routes in each of the physiographic regions. There was a decreasing tendency in the number *F. s. paulus* seen from 1965 to 1979.

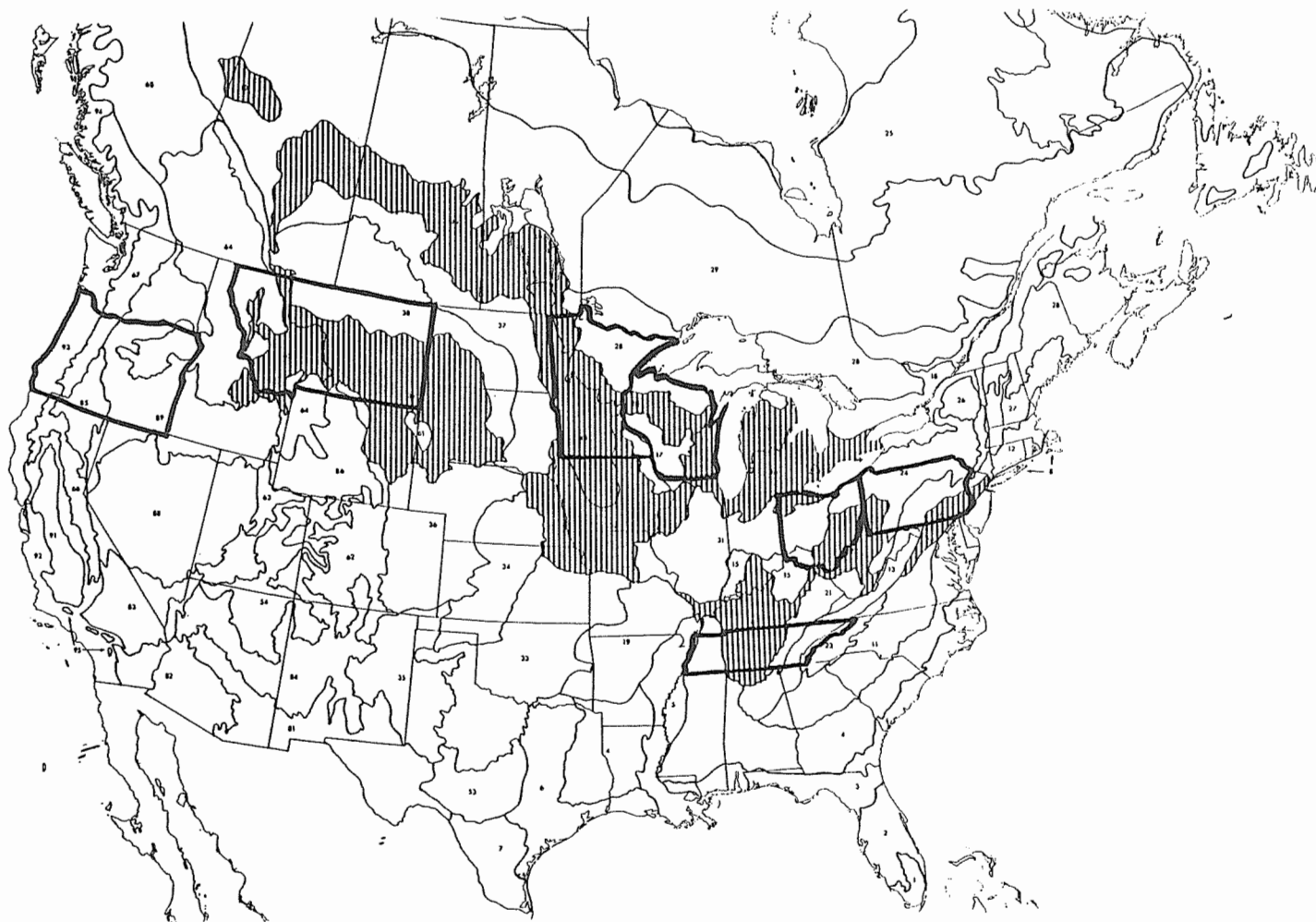


Figure 1: Physiographic strata and states in which a significant increase in American Kestrel counts occurred on Breeding Bird Surveys during 1968-1979.

Table 1: American Kestrels detected on Breeding Bird Survey (BBS) and on Raptor Routes (RR) on which observers drove continuously along the BBS route, surveying only for raptors.

		<u>BBS</u>	<u>RR</u>
East ^a	Number detected	59	52
	Number/hour ^b	1.0	1.6
West ^a	Number detected	41	27
	Number/hour ^b	0.9	1.9

^a Eastern states included DE, MD, NJ, NY, NC, PA, VA, WV, in which 90 routes were surveyed on which kestrels were seen on 25 BBS and 26 RR counts. Western states included AZ, NE, NM, ND, SD, TX, WY, in which 31 routes were surveyed on which kestrels were seen on 19 BBS and 12 RR counts.

^b BBS routes include 150 minutes of observation time. Eastern states RR observation times ranged from 48 to 136 min, $\bar{x} = 75$, western states 45 to 116 min, $\bar{x} = 71$.

American Kestrels were seen on 38 of the 121 special Raptor Routes. We compared the number of birds seen on the 1980 BBS routes and special RR. Volunteers saw about the same number of American Kestrels on BBS routes as on RR (ANOVA $p > .05$, Table 1). In the western states, more kestrels were counted on the BBS, a difference that might become significant with a larger sample. BBS routes have an observation time of 2.5 hours, and volunteers averaged 1.2 hours for the RR. Thus, in the eastern and western states the rate of detections was greater on the RR than on BBS routes.

DISCUSSION

The 15-year summary of the BBS data suggests the continental numbers of American Kestrels have increased during 1966-1979. Analyses of physiographic and state/province strata indicate that some areas are largely responsible for the increase in the U.S. and southern Canada, and that only in Illinois and Arkansas have kestrels declined. In the American Birds Blue List (published since 1971) of species apparently declining in numbers, there has been concern about the American Kestrel in various regions: Pacific Coast, Central and Southern regions (1974), Central and Southern (1976), New Jersey and Middle Atlantic Coast region (1977), Middle Atlantic Coast, Gulf, Appalachia and Ontario (1978), and "throughout the East and South a rather pronounced and prolonged population decline is being witnessed" (1979). These generalizations are not supported by the BBS. Generally, American Kestrel numbers are stable or increasing along BBS routes.

Special intensive surveys should be conducted in locales where more extensive surveys are inadequate. The Blue List has consistently expressed concern about *F. s. paulus* in Florida, but there are too few BBS data to allow analysis of trends there. The concern expressed in the Blue List is supported by more detailed assessments in Florida (e.g., Hoffman and Collopy 1987).

Surveying on Raptor Routes, on which volunteers looked specifically for raptors while retracing their BBS route, did not significantly increase the counts of American Kestrels, although detection rates were increased. In the western states, the late morning surveys of raptor routes apparently occur after the time of day when kestrels are most visible (R. Patterson, M. Fuller, D. Bystrak, unpubl. data). We recommend use of the standardized methods employed on the RR, during which 2 observers look for birds of prey during continuous driving, in special surveys of American Kestrels. By driving continuously, more area can be covered, thus potentially increasing the sample. Surveys designed to detect a larger sample of American Kestrels should be conducted in states like Arkansas and Illinois, in which declines were found for BBS data, and in Florida, where BBS counts are low and there is concern about the subspecies *F. s. paulus*.

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POPULATION REGULATION IN KESTRELS

ANDREW VILLAGE

Abstract: A review of published information on population regulation in kestrels showed considerable variation in dispersion patterns both within and between species. Although there was some evidence linking kestrel dispersion and density to food supply throughout the year, and to food supply and nest site availability during the breeding season, the evidence was sparse and requires more support. Possible mechanisms for population regulation within and outside the breeding season are suggested, along with experiments which would test their validity during the breeding season.

The population ecology of raptors was thoroughly reviewed by Newton (1979) who concluded that, in most cases, breeding numbers were limited either by lack of food or nest sites, whichever was in shortest supply. Outside the breeding season, food supply alone was often the main limit to numbers. This paper reviews the evidence that these ideas hold for kestrels, and includes work done since Newton published his review. The aims are to establish common trends within the kestrel group, to highlight deficiencies in our knowledge, and to suggest possible mechanisms by which kestrel numbers are regulated according to resource availability.

Much of what follows is based on my own work on Eurasian Kestrels (*Falco tinnunculus*) over the past 10 years. From 1975-80 I worked at Eskdalemuir in south Scotland, in an area of rough grassland planted with young conifers; whereas more recently I have collected similar data in arable farmland in south-east England. I have also included relevant work on Eurasian or other kestrel species, though for many of them, little or nothing has been published on density and dispersion. I have used the same definition of the kestrel group as Cade (1982). Most of these small falcons inhabit open areas of grass, farmland or scrub, and feed on small mammals, birds, lizards or insects.

DISTRIBUTION

The distribution patterns recorded to date for kestrels include **strict territoriality** (i.e., the whole range is defended and exclusive); **shared hunting ranges** (i.e., there is some overlap of part or all the home range, but birds of different pairs do not use the same area at the same time); and **flocking** (i.e., several birds hunt together in the same place) (Table 1). This wide variation is not solely due to differences between species, but also to differences within species according to time of year, habitat and particularly, food type.

Outside the breeding season. — The majority of kestrel species studied thus far tend to be territorial outside the breeding season, with territories held either by single birds or by pairs. Eurasian Kestrels held only individual winter territories in upland grassland (Village 1982a, 1985), but both individual and pair territories in arable farmland in south-east England (Pettiford 1983, A. Village unpubl. data). In the latter areas, lone territory holders were usually juveniles or adults that settled in the area after the breeding season, rather than the local breeders.

Table 1: Summary of dispersion patterns in kestrels.

Species	Time of year	Main habitat	Main prey	Dispersion of individuals	Dispersion of nests ^b	References
<i>F. araea</i>	B & NB ^a	Forest & scrub	Lizards (& insects)	Exclusive territories (pairs)	Regularly spaced	Watson 1981
<i>F. cenchroides</i>	Post-B	Mixed farmland & small woods	Insects	Exclusive territories (pairs) with nomadic juveniles	Not recorded	Genelly 1978
<i>F. naumanni</i>	B	Open grassland & farmland	"	Shared hunting range, some defence of nest	Colonial	Cramp & Simmons 1980
	NB	" "	"	Nomadic, shared hunting ranges & flocks	—	" " " Siegfried & Skead 1971
<i>F. rupicoloides</i>	B & NB	" "	Insects (& vertebrates when breeding)	Exclusive territories (pairs)	Regularly spaced?	Kemp 1978; Osborne & Colebrook-Robjent 1982
<i>F. sparverius</i>	B	Open grasslands farmland & scrub	Insects (& vertebrates)	Exclusive territories	Irregularly spaced?	Craighead & Craighead 1956; Phelan & Robertson 1978; Balgooyen 1976
	B	" "	" "	Shared hunting range, defence of territory around nest	Irregularly spaced & clumped	Cade 1955; Smith et al. 1972
	NB	" "	Voies (& insects)	Exclusive territories (pairs & singles)	—	Cade 1955; Craighead & Craighead 1956; Mills 1975; Phelan & Robertson 1978
<i>F. tinnunculus</i>	B	Open grassland	Voies	Shared hunting ranges, defence of territory around nest	Irregularly spaced & clumped	Cave 1968; Village 1982a, 1983
	B	Mixed farmland	"	Shared hunting ranges, defence of immediate nest area	Colonial	Peter & Zaumseil 1982
	B	" "	Voies & birds	Some overlap of hunting ranges, defence of territory around nest	Irregularly spaced	A. Village
	B	Arable farmland	Voies	Exclusive territories	Not recorded	Pettifor 1983
	NB	Open grassland & farmland	Voies & invertebrates	Exclusive territories (pairs & singles)	—	Village 1982 & unpubl. data; Pettifor 1983

^a B = Breeding season

NB = Non-breeding season

^b For definition, see text

Winter (or non-breeding season) territoriality seems to be common in other kestrel species, including *F. sparverius* in North America (Cade 1955, Enderson 1960); *F. rupicoloides* in Africa (Kemp 1978); *F. araea* in the Seychelles (Watson 1981) and *F. cenchroides* in Australia (Genelly 1978). In some of these species, concentrations of apparently non-territorial birds sometimes occur immediately after the breeding season, but these seem to be largely nomadic juveniles collecting temporarily at sites of local food abundance (Cade 1955, Cave 1968, Genelly 1978, Lett and Bird 1987). A noticeable exception to the general rule of winter territoriality are Lesser Kestrels (*F. naumanni*) which often gather in large flocks to feed on swarming termites or other insects, as do other insectivorous falcons such as *F. vespertinus*.

Distribution in the breeding season. - Distribution in the breeding season is more variable than in winter. Eurasian kestrels frequently share hunting ranges in the summer and defend only a small area around the nest, particularly where nest sites are clumped, but food is abundant (Cave 1968, Village 1982a). Defence of all the hunting range may be more frequent in farmland areas where food supply is poorer (Pettifor 1983), but ranges may still overlap more than in winter (A. Village unpubl. data).

Breeding season distribution in other kestrel species varies from those such as *F. araea* (Watson 1981) and *F. rupicoloides* (Kemp 1978), which seem to have exclusive territories, to those such as *F. naumanni* that show virtually no defence, even around the nest (Cramp and Simmons 1980). Reports of the distribution of American Kestrels during the breeding season differ, with some workers claiming exclusive territories (Balgooyen 1976, Phelan and Robertson 1978), and others reporting overlapping ranges with little or no defence (Cade 1955, Smith et al. 1972). Although this may reflect habitat differences, it needs further confirmation because the studies reporting exclusive ranges have not used marked birds and may have overlooked some overlap.

Nest distribution. - Kestrels do not build their own nests, but are restricted to abandoned stick nests of other species, tree-holes or cliff ledges. Even in species that can use a variety of sites, a single type often predominates in any one area, so nest distribution may largely reflect that of the preferred site (Osborne and Colebrook-Robjent 1982, Village 1983). Kestrel nest distribution patterns vary on a continuum which includes: **regular spacing** (i.e., occupied nests are spaced at similar distances from each other); **irregular spacing** (i.e., nests are spaced apart but by varying distances); **clumping** (i.e., a few nests may be very close together in a 'loose colony', but most are more isolated); and true **coloniality** (i.e., most pairs nest close to others and isolated nests are unusual). One of the few reported cases of regular spacing is in Seychelles Kestrels (Watson 1981) which maintain territories all year round and nest mainly in the bowls of palm trees. Such sites may be fairly widespread and abundant, thus allowing pairs to space their nests at regular intervals. Irregular spacing or clumping is usually seen in Eurasian Kestrels (Village 1983), though this species will sometimes form loose colonies where there are large numbers of closely adjacent sites, either on cliffs (Fennell 1954), in Rook (*Corvus frugilegus*) colonies (Piechocki 1982), or on man-made structures (Peter and Zaumseil 1982, Piechocki 1982). Even in colonies with nests only a few meters apart, there is usually some defence of the nest itself, and territorial behavior was thought to be involved in regulating one German colony that varied from 10 to 28 pairs over 18 years (Peter and Zaumseil 1982). Fighting over nest sites sometimes occurs between Lesser Kestrels, which are almost invariably in colonies of up to 500 pairs. It is much less obvious in Eurasian Kestrels and may not be involved in limiting breeding numbers (Cramp and Simmons 1980).

To some extent, the wide variability in distribution within the kestrel group seems to relate to their food and nesting requirements, as predicted for all raptors by Newton

(1979). For example, the flocking and colonial nesting of Lesser Kestrels is probably a reflection of their dependence on patchily distributed insect prey; and the variation in nest distribution within Eurasian Kestrels usually corresponds to variation in nest site availability. However, not all the observed variation is easily explained. American and Greater Kestrels often maintain exclusive territories, even when they are feeding almost entirely on insects (Balgooyen 1976, Kemp 1978). Similarly, some of the range overlap in Eurasian Kestrels occurs even when nests are some distance apart and cannot be entirely explained by the distribution of nest sites.

Although food and nest sites may ultimately be factors affecting kestrel distribution, their effects may not be direct, and individuals may respond in subtle ways according to the overall costs and benefits of any one distribution pattern. Thus, for any given density, a population may distribute itself either in small exclusive territories, in large overlapping ranges, or some mixture between the two.

Defending exclusive hunting ranges must cost in terms of time and energy, but may benefit by reducing prey depletion or disturbance by other birds. Overlapping ranges increase the risk of prey depletion or disturbance, but may benefit individuals by reducing the effort needed to defend an area and by freeing them to wander more widely in search of patchy or widely dispersed food. Male Eurasian Kestrels vigorously defended an area around their nest early in the breeding season when they may have lost their mate or nest to other males, but wandered more widely once the females were incubating and there was less danger of being usurped or cuckolded (Village 1980, 1982a). This change in behavior also coincided with greater food demands on the male and, in many cases, to a change to a more avian diet (Village 1982b). In this species, as in others, more work is needed to decide which of these factors, if any, are most important in affecting distribution patterns. Such work could include experimental manipulation of nest sites and/or food distribution to determine their effect on range overlap and territorial behavior. This may show, for example, whether range overlap is simply a function of how close adjacent pairs are, or whether it is also related to the ease of obtaining food.

REGULATION OF WINTER DENSITY

Winter food supply as a limiting factor. - Newton (1979) suggested that, for most raptors, food supply is likely to be the ultimate factor determining winter range and density. This seems to be true for kestrels which tend to winter in areas where food is more abundant. Thus Eurasian Kestrels migrate out of the most northerly parts of their range and winter in the milder climates of Eurasia, Africa and the Americas. Wintering at high latitudes is probably limited by the reduction of food supply caused by prolonged snow cover. A reduction in daylength may also leave insufficient time for hunting even in some areas that are not invariably snow-covered all winter.

Where kestrels are able to persist through the winter, prey density may affect the numbers found in any one area. At Eskdalemuir, kestrel numbers were positively correlated with vole numbers during the autumn and winter (Fig. 1). High kestrel numbers in good vole years were associated with more juveniles settling in autumn and persisting longer through the winter (Village 1985). To my knowledge, this latter study is the only one that has demonstrated a positive correlation between kestrel numbers and food supply outside the breeding season. Craighead and Craighead (1956) and Phelan and Robertson (1978) measured the size of whole raptor communities ("guilds") in successive winters in separate parts of North America. Both found a positive relationship between total raptor numbers and vole numbers, but this did not hold when American Kestrels were examined in isolation, even though voles were their main prey. This implies that

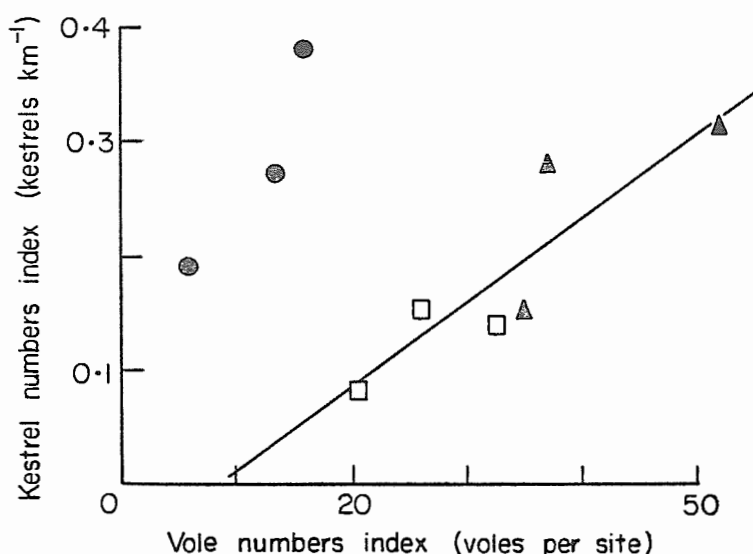


Figure 1: Relationship of kestrel numbers to vole numbers at Eskdalemuir, south Scotland, 1976-78, after Village (1982a). Kestrel numbers were measured by roadside counts in summer (circles), autumn (triangles), and winter (squares). Line is the regression fitted to autumn and winter values only: $Y = -0.062 + 0.007(\pm 0.002)X$, $df = 4$, $P \leq 0.05$.

interactions with other vole-eating raptors may have had important effects on kestrel density.

In most areas the wintering population includes permanent residents (remaining from the previous breeding season), as well as migrants which stay for varying periods during the winter (Enderson 1960, Cavé 1968, Mills 1975, Village 1985). Population density will depend on the balance of how many breeding birds remain on their territories, how many incomers settle, and how many individuals are able to persist through the winter. There is comparatively little known about what regulates the following 3 factors:

(a) Whether breeding birds stay on their territories may depend on other factors besides direct food shortage. Where some or all of the breeding population leaves for the winter, migration is usually started before food becomes scarce. At Eskdalemuir, most breeding birds have left even though vole numbers were at their seasonal peak around that time. Nearly all individuals that migrated in one year would do so in following years, provided they had returned to breed (Village 1985). There was thus a clear distinction between year-round and summer-only residents, suggesting that, for any individual, the decision to migrate or not may depend on age, previous winter experience or genetic factors.

(b) The rate at which incomers settle in an area varies during the winter and is usually highest during the immediate post-breeding period. The summer population is replaced by varying numbers of incomers, usually juveniles, but often includes some adults that may or may not have bred the previous summer. At Eskdalemuir, such settling was over by November, and I recorded no new arrivals thereafter. Birds which disappeared in mid or late winter were never replaced by newcomers, and their vacated

range was often filled by a neighbour expanding to fill the gap (Village 1982a). In south-east England, an apparent wintering area for some northern breeding birds, new settlers were recorded much later in winter, though only 3 of 10 territory holders removed in mid-winter were replaced, and then only temporarily (A. Village unpubl. data). Thus, even in areas where transients pass through during most of the winter, the density of wintering birds may be largely determined by the numbers settling in the period immediately after the young disperse, minus subsequent losses. Virtually nothing is known about behavior and population dynamics during late summer and early autumn. There seems to be a great deal of aggression among juveniles in early autumn, though it is several months before they are able to effectively defend a territory. They may spend the intervening time wandering and collecting at sites of local food abundance (Cade 1955, Lett and Bird 1987, A. Village unpubl. data).

(c) Once the population has settled in autumn, subsequent density is mainly determined by the rate of loss through mortality or emigration. In Scotland where the main prey, Short-tailed Voles (*Microtus agrestis*), declined over winter, there was a corresponding decline in kestrel numbers which, judged by ring recoveries, resulted from some birds dying on their territories and others moving some distance away. Such losses may be directly due to lack of food, so food supply could be both the ultimate and proximate factor regulating numbers, as suggested by Newton (1979). Where deaths occur that are not even indirectly related to food supply (such as a proportion of predation and accidental deaths), and birds are not replaced, the population will become lower than the local food supply can support. It could then remain below carrying capacity until the arrival of spring migrants. This might be one reason why numbers in some areas can increase rapidly in spring before there is any apparent increase in food supply (Village 1982a).

Territorial behavior in winter. - The role of territorial behavior in regulating winter numbers is not clear. Early in autumn when many birds may be trying to settle in an area, the aggression of residents might prevent them from doing so. The numbers able to settle could be related to food if high food supply reduced the aggression of, or area defended by, residents and/or increased the persistence with which incomers tried to settle. Once the main settling period is over, few vacated territories are subsequently reoccupied. This is true both for territories vacated naturally, where the disappearance and subsequent range expansion by neighbours may be due to food shortage, and when birds are experimentally removed from territories, where food shortage is not implicated (Village 1982a, A. Village unpubl. data). Thus birds may rarely settle on territories in mid-winter simply because too few are moving around looking for a territory at that season. Kestrels sometimes expand rapidly into the vacated range of a neighbour, which suggests that territory size in winter may be determined by the prevailing kestrel density, rather than directly by food supply. This idea is also supported by data from Eskdalemuir in early spring when territories decreased in steps according to how many kestrels had settled in the area, rather than gradually. The latter might be expected if territory size was directly dependent on the slowly increasing food supply (Village 1982a).

Thus, although there are some quantitative data linking kestrel winter numbers to food supply, there is virtually nothing to indicate how this link is achieved. Further work is needed to better establish the correlation of kestrel numbers and food supply in winter, and to elucidate the role of proximate factors such as the rate of settling, territorial behavior and subsequent losses. Other factors, besides food, that may influence winter density include the availability of perches or roosts (Mills 1975) or nesting sites (Village 1982a). While these may be important prerequisites within a winter territory, they have

not been conclusively shown to limit density below the available winter food supply. Experimental provision of perches or roosts in open areas may demonstrate that these factors are important limiting factors in some areas.

REGULATION OF BREEDING DENSITY

It would be surprising if the mechanisms of population regulation during the breeding season were not, at least to some degree, similar to those in winter. Once again, food is likely to be an important factor, though the breeding segment of the population has the additional requirement of finding somewhere to nest. Nearly all the work done on kestrels in summer has been exclusively concerned with finding breeding birds, so what follows applies to the regulation of breeding numbers, rather than the population as a whole.

Food supply as a limiting factor. – As Newton (1979) pointed out, the evidence suggesting that food limits the breeding density is based mainly on correlations between annual fluctuations of kestrel numbers and that of their main prey (Cavé 1968, Rockenbauch 1968, Snow 1968, Hagen 1969, Ziesemer 1973, Village 1982a). Cavé (1968) was able to investigate the effects of rainfall, temperature and vole numbers on kestrel breeding numbers using multiple regression. He found a significant negative correlation between numbers and rainfall and a significant positive correlation with temperature, but surprisingly, no correlation with vole numbers. However, he considered that this was due to his poor measure of food supply, and concluded that food was nonetheless important and that the correlations with weather were due to its effects on food supply or energy requirements. At Eskdalemuir, kestrel numbers were higher in good vole years than poor ones, though the correlation was not quite significant, probably because of the small number of years involved (Fig. 1).

One line of evidence which was not previously available for kestrels concerns variation in breeding density between habitats of different quality. One reason for this is that many published estimates of kestrel breeding density are unreliable (Village 1984), so it is seldom possible to compare studies made by different workers. However, comparable data I have collected from 3 areas of similar size but different habitat showed highest kestrel densities in those areas with the greatest proportion of habitat suited to voles, their major prey (Table 2).

Table 2: Breeding density of Eurasian Kestrels in 3 habitats with varying amounts of vole habitat.

Habitat	Size of study area (km ²)	Suitability for voles	Breeding density (pairs/100 km ²)
Upland grassland	100	High	33
Mixed farmland	111	Medium	24
Intensive arable farmland	83	Low	11

Table 3: Anecdotal and experimental evidence for the existence of a non-breeding surplus of kestrels.

Species	Replacement of birds lost naturally or shot	Replacement of experimentally removed birds late in season	Occupation of nest-sites made available	References
<i>F. araea</i>	–	Both sexes	–	Watson (1981)
<i>F. naumanni</i>	Females			Lucanus (1937)
<i>F. sparverius</i>	Both sexes Female	Both sexes		Mayr (1938) Enderson (1960) Bowman and Bird (1986)
<i>F. tinnunculus</i>	Injured Female	Both sexes	Occupation of crow nests after crows shot 10 experimental late nests 1 late nest box	Piechocki(1982) Village (1983) D. Masman (pers. comm.)

Nest site availability as a limiting factor. – Since kestrels do not build their own nests, and will readily take to man-made sites, nest site availability is more amenable to experimental investigation than in other raptors. Numerous studies have shown that putting nest boxes in areas of good hunting habitat with few or no natural sites can increase the numbers breeding there (Cavé 1968, Hamerstrom et al. 1973, Village 1983 and others). In some cases the results have been spectacular. Cavé (1968) increased breeding numbers in recently reclaimed polder from less than 20 pairs in 1959 to 109 pairs in 1960 by erecting nest boxes in the intervening winter. The occupation of artificial sites does not always mean that density has increased and it is necessary to check that birds have not simply moved from their natural sites into the better alternative provided.

Causes of non-breeding. – The occupation of artificial sites has shown that, in some areas, breeding density is held below the carrying capacity of the available food by shortage of nesting places. This does not necessarily mean that some individuals are prevented from breeding altogether by lack of a nest because birds may simply move to other areas where sites are available. It shows only a limitation of density in that particular area. Evidence for a genuine surplus of non-breeding birds comes from cases where one or both members of a breeding pair are removed during the breeding season and are subsequently replaced by new birds that breed (Table 3). When the replacements occur late in the normal breeding season, it is reasonable to assume that the incoming birds would not otherwise have bred because they lacked either a suitable territory, or partner or nest site. These possibilities can be distinguished by a similar type of experiment which involves erecting nest sites late in the season after pairs have already settled on their territories and started to breed. Subsequent occupation of such 'late nests' shows that birds were prevented from breeding solely by lack of a nest site,

Table 4: Summary of experimental evidence to determine the main factors limiting kestrel breeding numbers.

Factors which might limit breeding numbers	^a Experiment(s) needed to demonstrate given factors are limiting breeding numbers				
	Remove breeding birds from their territories late in the season, after all pairs have settled		Provide nest-sites late in the season after all pairs have settled on their territories		
	One member of breeding pair	Both members of breeding pair	Within territories of breeding pairs	Outside territories of breeding pairs	^b Provide extra food for unpaired non-breeding birds
Lack of nest-sites and/or suitable territories and/or suitable partners	+ ^a	-	-	-	-
Lack of nest-site and/or suitable territory	-	+ ^a	-	-	-
Lack of a nest-site due to overall shortage of natural sites	-	-	+ ^a	+ ^a	-
Lack of nest-sites due to territorial behavior of existing pairs	-	+ ^a	+ ^b	+ ^b	-

Other conditions which must be fulfilled	“Outcome of experiments that would demonstrate factor(s) being tested were limiting breeding numbers	Conclusions that could be drawn if outcome was as shown
	a. Removed bird replaced by another that subsequently breeds with the remaining partner.	There was a surplus of non- breeding birds unable to breed because they lacked a nest site, territory or partner.
	a. Removed pair replaced by new pair that subsequently breeds.	As above, but non-breeding <u>not</u> due to lack of a partner.
No surplus of usable natural sites	a. Occupation of late nest-sites by pairs that subsequently breed.	Non-breeding had sufficient food to breed but lacked a nest-site.
Surplus of natural nest-sites, but only within existing kestrel territories	a. Removed pair replaced by another that subsequently breeds. b. Breeding at late nest-sites but only <u>outside</u> existing kestrel territories.	As above but shortage of nest-sites due to non-breeders being excluded from sites within territories of breeding pairs.

Table 4 (ctd.)

Lack of food due to insufficient good hunting areas	-	+ ^a	-	+ ^b	+ ^c
Lack of food due to poor hunting ability of non-breeders	+ ^a	-	-	+ ^b	+ ^c
Lack of a suitable partner <u>alone</u>	+ ^a	+ ^b	+ ^c	+ ^c	+ ^d

+ = Experiments needed in each case. Letters a-d refer to the outcomes listed in column 8.

^a Experiments should be done sufficiently late in the season so that all pairs that would normally breed have started to do so.

^b Where extra food can be provided, it should be given to unpaired individuals that show no signs of pairing that year. Paired birds cannot be recognized as non-breeding until the very end of the laying period, by which time feeding may have no effect anyway.

^c Where evidence is based on a negative response (i.e., no subsequent breeding following a removal), it should be accepted only after sufficient trials to ensure a fair chance of a positive response.

Surplus of natural nest-sites outside existing territories	<ul style="list-style-type: none"> a. Removed pair replaced by new pair that subsequently breeds. b. No breeding at late-nest-sites, though they may be occupied by pairs. c. Feeding non-breeders results in breeding at natural nest-sites. 	Non-breeders confined to poor food areas that could only support breeding if extra food given. Non-breeders able to hunt well enough to breed in 'good' territories.
" "	<ul style="list-style-type: none"> a. Removed bird <u>not</u> replaced by another able to breed with original partner. b. No breeding at late nest-sites, though they may become occupied by pairs. c. Feeding non-breeders leads to breeding at previously existing natural sites. 	As above but non-breeders unable to breed even on good territories. Food shortage thus due to inability of non-breeders to catch enough food in prevailing conditions.
" "	<ul style="list-style-type: none"> a. Where one member of pair removed, the other re-mates and breeds with a new partner. b. Where both members of pair removed, no subsequent breeding by new pair, even if they occupy the territory. c. No breeding at late nest-sites. d. Feeding non-breeding birds does not induce pairing and breeding 	Non-breeding birds unable to breed because they lacked a suitable partner.

rather than lack of a partner or territory. Experiments at Eskdalemuir showed that, at least in Eurasian Kestrels, shortage of nest sites alone can prevent some individuals from breeding (Village 1983). American Kestrels removed from territories have also been replaced by birds that subsequently bred (Bowman and Bird 1986). Watson (1981) removed Seychelles Kestrels from their territories and all were eventually replaced, though removals were done in the pre-lay period, so it was not clear if replacements would otherwise have bred elsewhere.

Mechanism of breeding density regulation. - The exact mechanism of breeding density regulation may vary between species and even within species between different areas, involving a complicated interaction of factors such as food supply, territorial behavior and nest-site availability. In Eurasian Kestrels, Cavé (1968) thought that territorial behavior could not be involved in limiting breeding density because nests were much further apart than the radii of kestrel territories he measured (330 m for nests versus 25-35 m for territories). However, he used attacks on stuffed dummies to measure territory radius, which is a poor substitute for using live birds (Cade 1955). At Eskdalemuir, territory radius, as measured by observed combats between neighbours, was much larger, varying from an average of 300 m in a good vole year to 560 m in a poor one (Village 1983). Territories often included a number of vacant, usable nest sites, and it seemed that territorial behavior was causing a shortage of nest sites that prevented some birds from breeding in some years. Territory size was itself inversely related to vole numbers, so food supply was probably the ultimate limit to breeding numbers with its effect mediated through the proximate factors of territorial behavior and nest site availability. Residents were apparently no less aggressive in good vole years than poor ones, and territories were probably smaller in good vole years because incomers were more persistent in their attempts to settle at nests within the territories of existing residents (Village 1983).

Different mechanisms may apply to Eurasian Kestrels in other areas, or to other species. Where all the hunting range is defended, birds may be prevented from breeding by being excluded from suitable hunting ground rather than from suitable nest sites. In such circumstances non-breeding birds would breed in vacated territories, but would not respond to late nest sites put up in their original home range. Alternatively, non-breeding birds may not be able to catch enough food to come into breeding condition, whatever territory they are in. This may lead to replacement at vacated breeding territories by birds that are unable to breed themselves, even in good territories. In this latter case, individual competence may play a significant part in deciding whether a bird is able to breed. These different possibilities could be distinguished by a careful combination of removal and late-nest experiments (Table 4).

CONCLUSIONS

Although most kestrel species are roughly similar in size, morphology and habitat requirements (Cade 1982), they show remarkable diversity in their distribution, density and population dynamics. This is evident from the limited range of species so far studied, and is likely to be confirmed as more unusual species are examined and familiar ones are studied in a wider range of habitats. Perhaps the main unifying trend in the population regulation of kestrels is their diversity - which reflects the ability of species to adapt behavior to suit local conditions. The regulation of kestrel numbers seems to depend on the interplay of many factors which may vary with species, locality and time of year. These factors include prey density or availability, territorial behavior, nest site availability, the number of transients trying to settle, emigration and mortality rates, and the age structure of the population. Many of these are intercorrelated, and it is

likely that food supply is often the single ultimate limiting factor. However, even when this is true, there is still much to be learned about the role of other proximate factors.

There are several areas where further effort could be usefully directed:

1. There is still a serious lack of information on basic population dynamics, and particularly on the relationship of kestrel numbers to prey numbers. A correlation between the two is widely assumed, but comparatively few studies have measured both simultaneously for long enough to tell if this is generally so. The problem is particularly acute for the less widely distributed species, for which there is not even basic information on density or distribution.

2. Further detailed work is needed for the better known species, especially during the post-breeding period, which may be a crucial time for the regulation of winter numbers.

3. Correlations obtained from simple observations should be tested, wherever feasible, by field experiments. This is possible during the breeding season by manipulating nest site and food availability, and by using removal experiments to show if the method of population regulation proposed for Eurasian Kestrels in upland Scotland (Village 1983) holds for other species.

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NESTING SUCCESS OF THE AMERICAN KESTREL (*Falco sparverius sparveriioides* Vigors) IN THE BOCA DE LA JAULA, TAPASTE, HAVANA PROVINCE

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Abstract: In a 416 ha study area, 42 nests were found, all but one in the defoliated tops of palms. Only 18 nests subsequently held eggs. Nests were an average of 15.9 m above ground, having a mean diameter of 38.9 cm and a mean depth of 52.5 cm. Of these nests, 32.5% were abandoned when the nest palms were cut down, 18.6% abandoned due to human disturbance, and 4.6% failed due to predation. Clutch size averaged 2.78 eggs and mean egg width and breadth were 34.4 cm and 27.4 cm, respectively. Laying occurred between 8 April and 25 May, hatching between 27 May and 13 June, and fledging between 11 June and 29 July. Causes of hatching failure were: pesticides (25% of all eggs laid), disturbance (8.3%), predation (4.1%), congenital deformity (2.0%), accident (2.0%), and unknown causes (6.2%). Man was the principal cause of egg loss, directly or indirectly accounting for 59%. Nestling production per nest with eggs was 1.90. Fledging success was 52.9%, but total nesting success was only 37.5%. Nestlings were fed predominantly *Anolis* spp. lizards, but bats and small rodents were taken by breeding adults.

The American Kestrel is the most common species of Falconidae found in Cuba. Among the Falconiformes, only the Turkey Vulture (*Cathartes aura*) exceeds it in abundance and distribution (Garrido and Garcia Montana 1975). Despite this, only Gundlach (1893) has made observations on the nesting of the kestrel in Cuba. This paper presents further data on Cuban kestrels. Observations were made by the first author during the summer of 1980 in the area of Boca de la Jaula, Tapaste, Havana province.

METHODS AND MATERIALS

The 416 ha study area, part of the northern boundary of the Valley of Peru, was characterized by small calcite hillocks, such as those known regionally as the Stairway of Jaruco. It also included an extensive plain, the Valley of Peru, which is crossed by ditches for the overflow pipes of the Manposton Dam. The hillocks are covered by typical vegetation, predominantly Fan Palms (*Coccothrinax mariguana*). The plains are comprised mainly of dairy cattle pastures with isolated trees of the following: Royal Palm (*Roystonea regia*), Almacigo (*Bursera simaruba*), Avocado (*Persea americana*), Carolina (*Pechira insignis*), Abey (*Lysiloma bahamensis*), Cedro (*Cedrela mexicana*), Ceiba (*Ceiba petrandia*), Chirimoya (*Annona cherymolis*), Eucalyptus (*Eucalyptus resinifera*), Mamey (*Calocarpus sapota*), Mango (*Mangifera indica*), Cercas de Pinon Amorosa (*Gliricidia sepium*), and Yagruma (*Cecropia peltata*). Geographically, the study area is located at 23 02'N and 85 05'W, in the township of Tapaste, province of Havana.

Nests were located by observing the frequency of adult activity in topless palms. This also served to indicate the stage of nest development. To determine if there were eggs, the nests were inspected 2 weeks after we first noticed activity. This allowed time for the completion of the clutch and minimized disturbance. Nests in which eggs were found were examined a second time 20 days later to determine hatching success. Thereafter, weekly observations followed nestling development. Nest inspections entailed climbing the palm

and examining the interior of the nest with a convex mirror attached to a metal pole. This was generally so brief that the activity of the adults was uninterrupted. Seven nests accessible from the highway were checked at 3-day intervals to determine specific dates of nesting activity, however this attracted the attention of curiosity seekers, eventually bringing about the theft and death of several nestlings. Moreover, it was not possible to surround the tree trunks with naphthalene crystals and predators, likely rats, were able to follow our scents and attack several nestlings.

Nest characteristics were measured at the end of nesting activity. Depth, the distance from nest entrance to the center of the floor, and the diameter of the nest at the entrance level, were measured in centimeters. Prior to fledging, young were marked with colored cloth strips, with a different color for birds of each nest.

RESULTS AND DISCUSSION

A total of 42 nests was located, all in Royal Palms. One nest was in a trunk cavity, however all the rest were located in depressions at the top of defoliated palm trunks. These depressions are caused by the rapid rotting of the pithy core leaving walls of the more fibrous exterior. Gundlach (1893) reported that Cuban kestrels nest in holes in palms and other trees, as well as in cavities in walls and cliffs. Fisher (1893) stated that 20 feet (ca. 6m) was the minimum nesting height required by these kestrels. Our lowest nest was 6.5 m (Table 1), thus supporting Fisher's finding. Nest depressions ranged from 22.0-51.0 cm in diameter to 23.0-92.0 cm in depth (Table 1). The nest substrate consisted of feathers, bits of cloth, excrement, food remains, and rotting wood. Typical of other *F. sparverius* subspecies, there appeared to be no construction to the nest. Similar nest parameters and substrates have been reported for *F. s. sparverius* (Sherman 1913, Bent 1938).

Nesting commenced in late March to early April. Laying dates ranged from 8 April to 25 May and hatching took place from 27 May to 13 June. Fledging occurred between 11 June and 29 July. Mean incubation and fledging times were 28.2 and 29.1 days, respectively. Some nests prematurely fledged young due to researcher presence and these nests were excluded from the analyses.

Of 42 nests, 14 were destroyed early in the courtship period when the nest trees were cut down. Adults abandoned 8 other nests for unknown reasons and 2 nests were abandoned after interspecific encounters with a pair of Red-tailed Hawks (*Buteo jamaicensis*) and Turkey Vultures, respectively.

The average clutch size of 2.78 is considerably smaller than those reported for other kestrel subspecies. Balgooyen (1976) found a mean clutch size of 4 for *F. s. sparverius* in northern California while Bent (1938) reported 4 eggs to be "the most common number found" for *F. s. paulus* in north Florida. This discrepancy is however, consistent with the trend towards smaller clutch sizes in tropical birds (Lack 1968). Egg dimensions (Table 1) were not dramatically different from those reported for other subspecies, i.e., *sparverius*, *peninsularis*, *paulus*, and *phalaena* (Bent 1938).

In 5 of 18 nests (28.0%) we found soft-shelled eggs and in 4 of these we also found thin-shelled eggs with less pigmentation than normal. In all, 9 soft-shelled and 5 thin-shelled eggs were found (29% of all eggs laid). Of these 5 clutches, only 5 of 16 eggs hatched and only 2 nestlings successfully fledged. Thus there was 87% mortality of all eggs laid in those clutches. Only 3 of 32 eggs failed to hatch in other clutches. Overall hatching success was 70.1% which was low compared to a mean hatching rate of 89.3% reported for *F. s. sparverius* (Balgooyen 1976). Since soft- and thin-shelled eggs coincided in the same clutch, it may be that the same agent is responsible. Intensive use of pesticides, especially DDT, is common in the study area and these pesticides are

Table 1: Quantitative values of the nests, eggs, and productivity of *Falco sparverius sparverioides* of the Boca de la Jaula, Tapaste, Havana Province, Cuba.

Measurement	X	Range	N	S.E.	C.V.
Nest height (m)	15.9	6.5 – 28.0	18	1.58	6.69
Nest diameter (m)	38.9	22.0 – 51.0	16	2.06	8.23
Nest depth (cm)	52.5	23.0 – 92.0	18	4.09	17.23
Clutch size	2.1	1.0 – 5.0	18	0.22	0.96
Egg length (mm)	34.4	32.0 – 36.5	39	0.20	1.26
Egg breadth (mm)	27.4	26.0 – 30.0	39	0.13	0.80
Nestlings hatched per nest	1.90	1.0 – 5.0	18	0.23	0.96
Fledglings per nest	1.20	0.0 – 4.0	15	0.22	0.86

known to affect eggshell thickness (Ratcliffe 1967, Hickey and Anderson 1968, Porter and Wiemeyer 1969). The decreased hatching success of clutches with soft- or thin-shelled eggs suggests that pesticides may be adversely affecting *F. s. sparverioides* populations.

Of 34 nestlings hatched, only 18 fledged for a fledging success of 52.9% (Table 1). Total nesting success was only 37.5%. The number of nestlings per nest ranged from 1 to 5, but the median was 1.9. Others have reported 3-7 nestlings per nest for *F. s. sparverius* (Fisher 1893, Pearson 1936, Bull and Farrand 1977). Nestling mortality resulted from abandonment (4), hunting (4), predation (2), congenital deformation (1), cannibalism (1), accidental (1), and unknown causes (3). Cannibalism occurred when the last hatched chick in a clutch of 3 was consumed by its nest mates. Cannibalism has not been previously reported in this subspecies. The feet of several nestlings were consumed by either ants or rats. The dead young appeared to have been ejected from the nest by the adults.

We made occasional observations of prey deliveries by adults to nestlings. Prey consisted predominantly of small lizards (*Anolis* spp.). We also observed adult kestrels pursuing bats and small rodents as they emerged from cavities in palm trunks early in the morning. Several wings and bones of unidentified ducks were found in nests, but it is not known if they were captured or even eaten by kestrels.

We noted that the bat hunting method employed by *F. s. sparverioides* differed somewhat from that described for *F. s. sparverius* (O. Garrido pers. comm.). The Cuban Kestrel perches near the roost of the bats and stoops on them as they emerge whereas the northern subspecies captures bats on the wing in the open.

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DISTRIBUTION AND NESTING ECOLOGY OF THE AMERICAN KESTREL (*Falco sparverius paulus*) NEAR ARCHER, FLORIDA

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Abstract: Historical records document the presence of nesting American kestrels near Archer, Alachua County, Florida during the late 1880's. Surveys in this area during 1981-1982 revealed that kestrel densities were higher in former and existing areas of the Longleaf Pine (*Pinus palustris*)-Turkey Oak (*Quercus laevis*) association (0.41 pairs/km²) than in areas of former and existing hardwood hammocks (0.14 pairs/km²). Nesting substrate was predominantly the Longleaf Pine (66% of 38 nest-sites). Nest cavities most often originated from *Colaptes* or *Melanerpes* woodpeckers.

In Florida, the American Kestrel is represented by 2 distinct populations. The nominate race, *F. s. sparverius*, occurs as a migrant and winter resident, whereas *F. s. paulus* constitutes the breeding population, and is thought to be a permanent resident (Howell 1932). In recent years, *F. s. paulus* has declined in numbers (Wiley 1978), and has been classified as "threatened" by the Florida Game and Fresh Water Fish Commission (FGFWFC 1981).

Published information concerning the kestrel's former and present status as a breeding species in Florida is limited. Howell (1932) considered *F. s. paulus* to be "locally common" in the state, preferring "open pine forests, wherever dead trees are found." Baynard (1913) described *F. s. paulus* as a "common resident and pretty evenly distributed throughout" Alachua County. Except for the recent study of Bohall-Wood and Collopy (1986), subsequent reports on this population have been largely anecdotal (MacFarland 1973, Norris 1976) or have failed to clearly separate *F. s. sparverius* and *F. s. paulus* (Sprunt 1954, Layne 1980).

Substantial unpublished information on *F. s. paulus* exists in the records and specimens of oologists active in Florida during the late 1800's and early 1900's. Specimens at the Florida State Museum indicated that T. Gilbert Pearson collected a number of kestrel egg sets near Archer in southwestern Alachua County, Florida, during the late 1880's. In the literature Pearson also refers to observations of kestrels near Archer (Pearson 1888, 1890, 1918, 1937; Dutcher 1920).

Because of the historical occurrence of kestrels near Archer, we chose to investigate the kestrel's current distribution and abundance in its vicinity. The objectives of the study were to (1) characterize the habitats occupied by *F. s. paulus*, (2) describe sites used for nesting, and (3) determine the migratory status of the *F. s. paulus* population in this area.

STUDY AREA AND METHODS

The oological records of T.G. Pearson were not sufficiently specific to locate his former collecting locations. Hence, we established a primary study area of 92 km² to include the 2 dominant plant associations near Archer: hardwood hammocks and Longleaf Pine (*Pinus palustris*)-Turkey Oak (*Quercus laevis*) sandhills. These vegetation associations are described in detail by Laessle (1942, 1958) and Veno (1976). Throughout

this paper, the 2 vegetation types refer to areas of existing hammocks and sandhills, as well as areas formerly occupied by these associations.

The hardwood hammock community is variable in its form, ranging from xeric hammocks of widely spaced Live Oaks (*Q. virginiana*) to mesic hammocks dominated by deciduous species. The latter variant is considered the climax forest in north Florida (Laessle 1942, Veno 1976).

Formerly present in this study area, pure Longleaf Pine stands could not be identified in the habitat analysis and are included as part of the hardwood hammock community. Just a few small (less than 10 acres) second-growth stands remain. Additionally, fire suppression has reduced the distinction between the Longleaf Pine flatwoods and the hardwood hammocks in some areas. Thus, the hardwood hammock community as herein defined, includes small Longleaf Pine groves and agricultural fields with scattered Longleaf Pines. Extensive areas of both hardwood and Longleaf Pine stands have been converted to either agricultural lands, commercial Slash Pine (*P. elliotii*) plantations or housing developments.

The Longleaf Pine-Turkey Oak association occurs on the higher undulating ridges, characterized by the Candler-Apopka soil association. Due to extensive logging and fire exclusion, Turkey Oaks now dominate many sites. Wiregrasses (*Aristida stricta* and *Sporobolus junceus*) are characteristic of the ground cover.

During 1981 and 1982, we searched the primary study area for kestrel pairs and nests, using ground and car survey techniques (Craighead and Craighead 1956, Fuller and Mosher 1981). No part of the study area was intensively studied both years. Because available information suggests that many kestrel breeding populations are relatively stable between years (Enderson 1960, Newton 1979, Craighead and Mindell 1981, Hoffman 1983), we felt justified in pooling the data from both years for analysis. However, the stability of kestrel breeding populations has not been rigorously documented.

While driving on roads throughout the primary study area, we scanned snags and likely perches for kestrels. Areas not visible by car were searched on foot. The entire study area was checked initially in late March to mid-April to locate occupied territories. Potential nest sites (dead trees with cavities) were examined.

We attempted to enumerate all breeding pairs and nests within the study area, and characterized each nest site by surrounding vegetation, substrate, and probable origin of nest cavity. Territories in which no active nest was located were characterized by dominant vegetation type in the feeding areas. The proportional distribution of kestrel nests in the 2 vegetation associations was compared to the proportional availability of each vegetation type in the study area using the Chi-square goodness-of-fit test (Siegel 1956).

Probable origin of nest cavity was determined based upon the descriptions of Dickson and Conner (1981) and personal experience. Distinction among cavities excavated by the Northern Flicker (*Colaptes auratus*), the Red-headed Woodpecker (*Melanerpes erythrocephalus*) and Red-bellied Woodpecker (*M. carolinus*) was not always possible, particularly for old, worn, and often enlarged cavity entrances. These unidentified cavities were considered to be constructed by "medium-sized woodpeckers."

We made additional observations of nesting kestrels in southwestern Alachua and northeastern Levy counties during 1981-1983, in an area roughly bounded by the roads joining Gainesville, Newberry, and Bronson. In 1982 and 1983, we used the same techniques employed in the primary study area on the kestrel breeding population on the 500 ha Berry Ranch, located 10 km northwest of Archer. This area is within the Longleaf Pine-Turkey Oak association, except for 100 ha which is intermittent wetland.

During May-August 1981 and January-March 1982, we color-banded adult and fledged immature kestrels to facilitate individual recognition. Birds were captured using bal-chatri traps baited with white mice (Erickson and Hoppe 1979). Despite repeated attempts to capture them in July and August, several adult and immature kestrels showed little or no interest in the bait.

We attempted to locate the wintering and subsequent breeding areas of birds banded in May-August. Kestrels banded in January-March were classified as to breeding status (mated or not mated), and attempts were made to locate the nest sites of these individuals. Only kestrels known to be *F. s. paulus*, distinguished by breeding behavior and late summer sightings, are considered here.

In 1983, we solicited copies of the data associated with American Kestrel egg sets from Florida to supplement the records of T.G. Pearson in the Florida State Museum. Museums contacted either held over 1,000 total egg sets or had Florida as an area of special representation (see Kiff 1979). Additionally, part of Pearson's collection is housed at his alma mater, Guilford College in North Carolina (Orr 1983, L. Moseley, pers. comm.).

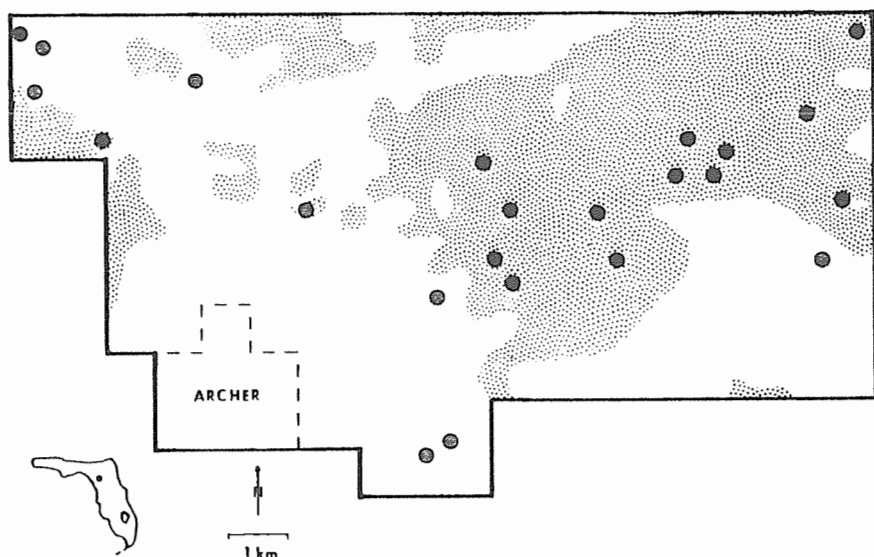


Figure 1: Location of primary study area, southwestern Alachua County, Florida. Black dots indicate American kestrel nests or territories during study period. Stippling indicates areas of former and existing Longleaf Pine-Turkey Oak vegetation type, areas of former and existing hardwood hammocks shown in white.

RESULTS

Habitat. - In the primary study area, nesting kestrels were found most frequently in the Longleaf Pine-Turkey Oak sandhills (Fig. 1). The hardwood hammock association comprised 60.0% (55.2 km²) of the primary study area, whereas the Longleaf Pine-Turkey Oak association comprised 40.0% (36.8 km²). In comparison, 35.0% ($n = 8$) of the kestrel nests (or territories) were in hardwood hammock areas and 65.0% ($n = 15$)

Table 1: Vegetation surrounding American Kestrel nest sites or territories, north-central Florida 1981-1983.

Vegetation type	Location ^a					
	PSA		BR		SWAC	
	n	(%)	n	(%)	n	(%)
Longleaf Pine-Turkey Oak (LP-TO) Association						
LP-TO forest	5	(22)	2	(20)	3	(18)
LP-TO forest/agricultural field edge	6	(22)	1	(10)	5	(29)
Scattered Longleaf Pines in agricultural field	2	(9)	7	(70)	3	(18)
Mowed lawn	2	(9)				
Hardwood Hammock (HH) Association						
HH/agricultural field edge	3	(13)			1	(6)
HH/residential area edge					2	(12)
Scattered Longleaf Pines in agricultural field	4	(17)			2	(12)
Open Longleaf Pine forest					1	(6)
Hedgerow through pasture	1	(4)				
TOTAL	23		10		17	

^a Locations are PSA=primary study area, BR=Berry Ranch, and SWAC=other areas in southwestern Alachua and northeastern Levy counties, Florida.

were in Longleaf Pine-Turkey Oak areas. This difference is significant ($\chi^2 = 6.09, p < 0.05$), indicating that kestrel pairs did not occur randomly in the study area. Breeding densities were 0.41 pairs/km² in the Longleaf Pine-Turkey Oak area and 0.14 pairs/km² in the hardwood hammock vegetation type.

The vegetation immediately surrounding kestrel nests in the primary study area indicated frequent nesting in association with pastures or cultivated farmland, or within areas of the Longleaf Pine-Turkey Oak forest (Table 1). A number of nest trees (26%, $n = 6$) were in cultivated fields or pastures which had been cleared except for occasional standing Longleaf Pines. In each of these fields, there were several dead pines with woodpecker cavities.

On the Berry Ranch 8 kestrel pairs were present during summer 1982, and 7 pairs were present during summer 1983. Ten individual nest trees were located. Pastures with isolated Longleaf Pine trees were the principal kestrel nesting habitat (Table 1). Breeding densities on the ranch were 1.6 pairs/km² in 1982 and 1.4 pairs/km² in 1983, although several pairs nesting near the borders of the ranch were observed foraging outside the property.

Table 2: American Kestrel nest sites, north-central Florida, 1981-1983.

Nest substrate	Location ^a					
	PSA		BR		SWAC	
	n	(%)	n	(%)	n	(%)
Longleaf Pine <i>Pinus</i> (sp.)	10	(48)	9	(90)	6 1	(86) (14)
Live Oak	3	(14)				
Turkey Oak	5	(24)	1	(10)		
Building	1	(5)				
Electrical station	1	(5)				
Bird box	1	(5)				
TOTAL	21		10		7	

^a Locations are as in Table 1.

In other areas of southwestern Alachua County and extreme northeastern Levy County, 17 kestrel nests or breeding territories were located during 1981-1983. Characterization of these sites indicated that kestrels occurred in areas similar to those occupied in the primary study and on the Berry Ranch (Table 1). In particular, kestrels nested in the Longleaf Pine-Turkey Oak plant association (65%, $n = 11$).

Nest sites. - In the primary study area, kestrels nested most frequently in Longleaf Pines (Table 2); Turkey Oaks and Live Oaks were occupied as well. Three nests in man-made structures were located, 2 of which were associated with electrical transmission facilities. Outside the primary study area, kestrel nests were almost exclusively in Longleaf Pines (Table 2).

Nest cavity origin of tree nests included old Northern Flicker cavities, old Pileated Woodpecker (*Dryocopus pileatus*) cavities, the cavities of "medium-sized woodpecker," or natural cavities (Table 3). Natural cavities were solely in Turkey Oaks, whereas all nest cavities in Longleaf Pines were of woodpecker origin.

Observations of color-banded kestrels. - Of the 8 adult kestrels color-banded in May-August 1981, 5 were located within 0.5 km of their breeding sites during the following winter and nested in the same area the following spring. The other 3 individuals were not relocated.

Of the 9 immature kestrels banded in July-August 1981, 2 individuals were subsequently located. One immature female wintered near its original place of banding, but disappeared in March. An immature male banded in August was not observed during the winter, but was located nesting 5 km east of its natal site the following spring.

Each of the 12 kestrels banded in January-March 1982 was associated with a kestrel of the opposite sex, and at least 9 nested within 0.5 km of the banding site. For 2 pairs, a slight habitat shift between winter and spring was observed. Both pairs fed over agricultural fields during the winter, and in spring frequented an area of Longleaf

Table 3: Probable origin of American Kestrel nest cavities, north-central Florida, 1981-1983.

Cavity origin	Location ^a					
	PSA		BR		SWAC	
	n	(%)	n	(%)	n	(%)
Northern Flicker	3	(14)	1	(10)	2	(33)
Pileated Woodpecker	1	(5)	2	(20)	1	(17)
Medium-size woodpecker ^b	10	(48)	7	(70)	3	(50)
Natural	4	(19)				
Man-made	3	(14)				
TOTAL	21		10		6	

^a Locations as in Table 1.

^b Includes cavities excavated by the Northern Flicker, Red-headed Woodpecker and Red-bellied Woodpecker.

Pine-Turkey Oak woods where they nested. This behavior was documented by Bohall-Wood and Collopy (1987) for kestrels inhabiting Longleaf Pine-Turkey Oak areas in north-central Florida. Observations by Layne (1980) in Highlands County suggested a similar trend.

Records of oologists. - The survey of museums and literature (Pearson 1888, 1890, Quaintance 1888) revealed that between 1887 and 1891 T.G. Pearson and A.L. Quaintance collected at least 36 kestrel egg sets, the locality of each being "near Archer" or "Archer," Alachua County, Florida. Additionally, Pearson referred to collecting 26 kestrel egg sets in 1890 near Archer (Pearson 1937). Of the extent egg sets, no more than 6 were collected in 1890. Therefore, the 2 men took at least 56 kestrel eggs sets during the 5 year period.

Pearson's descriptions of kestrel nesting habitat indicate association with pine forests (Dutcher 1920, Pearson 1937). Pearson does not however, clearly distinguish between areas of old-growth Longleaf Pine and the Longleaf Pine-Turkey Oak association. He refers to kestrel habitat as the "piney woods" (Pearson 1937:12) or the "pine-tree region" (Dutcher 1920:39).

According to Pearson (Dutcher 1920), kestrel nests were invariably found in old flicker cavities in dead trees. In the survey of museum collections, all egg sets which include data (n=16) were taken from cavities in dead trees; 4 egg sets are listed as being in old flicker cavities. The 4 egg sets in museum collections with mention of tree species were all in pines.

Pearson also noted the close attachment of pairs during the non-breeding season. He stated, "while not demonstrative in the least at this period they nevertheless remain in close proximity to each other, feeding frequently in the same field, and often roosting" together (Dutcher 1920:39).

DISCUSSION

American Kestrel breeding densities were higher in the Longleaf Pine-Turkey Oak association than in the hardwood hammock association, as found by Bohall-Wood and Collopy (1986) during road-side transects throughout north-central Florida. These results suggest differences exist in the suitability of sandhill and hammock areas for kestrel survival and reproduction. Potential differences that would affect the kestrel population include nest-site abundance, foraging area availability, and prey populations (see Newton 1976, 1979).

Elsewhere in the American Kestrel's extensive range, nest site availability has frequently been found to limit kestrel abundance (Smith et al. 1972, Hamerstrom et al. 1973, Balgooyen 1976, Stahlecker and Griesse 1979). At the Ordway Preserve in Putnam County, Florida, also comprising Longleaf Pine-Turkey Oak habitat, an average density of 2.1 pairs/km² (Hoffman 1983) suggests that kestrel abundance may be proximately limited by intra-specific territoriality (see Village 1987). The Ordway Preserve has a history of limited logging (Humphrey et al. 1985), however sandhill forests in the primary study area have been frequently logged and disturbed, resulting in reduced Longleaf Pine populations. The lower kestrel densities observed in these altered sandhill areas suggest nest site availability may be limiting kestrel populations, which could be investigated by provisioning of nest boxes in both vegetation types.

The open areas required by kestrels for foraging are the dominant feature of both present-day sandhills and hammocks. Therefore, the availability of potential foraging areas within each vegetation type should not limit kestrel populations. Sandhill forests are naturally open with a regime of regular burning. Fire suppression has caused some sites to have dense understories, particularly of fire intolerant Rosemary (*Ceratiola ericoides*); such sites may be unsuitable for kestrels and a program of controlled burning would probably be beneficial to kestrels inhabiting these areas. Hammock areas have been largely converted to agriculture, a frequent foraging area of kestrels throughout their range (Enderson 1960, Heintzelman 1964, Smith et al. 1972, Ganis 1976, Collopy and Koplin 1983).

The observations of Bohall-Wood and Collopy (1987) in north-central Florida suggest that differences in kestrel abundance between sandhills and hammocks may in part result from differences in prey populations. Kestrels in sandhill areas captured more vertebrate prey, primarily lizards, and had a higher capture success rate than birds foraging in hardwood hammock areas. Sandhill woodlands support an abundant lizard fauna, while intensive agriculture may reduce lizard abundance (McDiarmid 1978). Kestrels in hammock areas would be forced to consume more insects, thus returning less energy per unit of effort (Bohall 1984). Data on the time budgets and reproductive success of kestrels in both vegetation types would be useful in determining the effects of differences in prey populations.

The data are not available to assess the relative contributions of nest site availability and prey abundance on limiting kestrel breeding populations in sandhill and hardwood areas. However, the results of such an analysis would have important implications for active management programs; nest site availability can be manipulated using nest-boxes, while prey populations are very difficult to manipulate.

American Kestrels use a variety of nest sites in North America, including trees, buildings and cliffs (Cade 1982). The species of trees used differs among geographical regions (Smith et al. 1972, Smith and Murphy 1973, McClelland 1977, Raphael and White 1984). The frequent use of Longleaf Pine observed in this study indicates that this tree species is particularly important for kestrel nesting in north-central Florida. In favored sandhill woodlands, Turkey Oak snags frequently occur in the same areas as

Longleaf Pine snags, but because the oak is a much smaller tree, rarely growing more than 10 m tall, it may be a less preferred nest site. With the continued removal or poor reproduction of Longleaf Pine, and their absence in many sandhill areas, the Turkey Oak may be an important alternate nest site for kestrels and may in fact increase in importance because the Longleaf Pine is continually becoming scarcer in north-central Florida (Bechtold and Knight 1982).

Throughout its range the American Kestrel is frequently associated with the Northern Flicker, using its old cavities for nesting (Roest 1957, Smith et al. 1972, Raphael and White 1984); both species prefer open and semi-open areas (Hamel et al. 1982). In Florida, the Red-headed Woodpecker is a characteristic breeding species of open habitats (Howell 1932) and therefore a potentially important source of kestrel nest sites. Red-headed Woodpeckers were common in the primary study area, the Berry Ranch, and elsewhere in southwestern Alachua and northeastern Levy counties. Although direct use by kestrels of old Red-headed Woodpecker cavities was not observed, kestrels were found nesting in unaltered Northern Flicker and Pileated Woodpecker cavities. Due to difficulties in the identification of cavity origin, it was not possible to assess the extent to which kestrels used altered Red-headed Woodpecker cavities in the study areas. Elsewhere in Florida, kestrels avail themselves of the enlarged cavities of the Red-headed Woodpecker, while average-sized Red-headed Woodpecker cavities are too small (Hoffman 1983).

Observations of color-banded kestrels indicate that some of these birds are permanent residents in north-central Florida, maintaining year-round territories and pair bonds (see also Bohall 1984). Similar populations are found elsewhere in the southern part of the kestrel's U.S. range (Cade 1955, 1982). More extensive data comparing fidelity to both breeding sites and mates in sandhill and hammock areas would be useful in assessing the quality of these associations for kestrels. Newton (1979) noted that European Sparrowhawks (*Accipiter nisus*) in territories with good food conditions were philopatric, while birds in food-poor areas often changed territories between years.

Direct comparison of kestrel abundance between T.G. Pearson's era and the present is not possible because of the nonspecific definitions of his former collecting locations. The historical records document that the kestrel was common in the vicinity of Archer during Pearson's time. Today, a substantial population still exists.

In Pearson's era there were many areas of old-growth forest, including pure Longleaf Pine and Longleaf Pine-Turkey Oak. The extent to which the kestrel nested in these habitats is uncertain. Possibly the original clearing of the pine forests (and hardwood hammocks) for agriculture created habitat for the kestrel. However, Pearson (1937:12) referred to finding kestrels nesting in a "deadening", a term used to describe a group of dead trees within the old-growth Longleaf Pine forest (Schwarz 1907). Howell (1928) also mentioned that kestrels frequently nest within deadenings in the southeastern U.S.

In his only comments concerning changes in the kestrel's status in Florida, Pearson (1918) stated that a recent (circa-1918) visit to his boyhood haunts, an area of "original" (i.e., virgin) pine forest had been cleared, resulting in a decrease in populations of the kestrel, Red-cockaded Woodpecker (*Picoides borealis*), and Brown-headed Nuthatch (*Sitta pusilla*). He described these pine-inhabiting species as being replaced by Loggerhead Shrikes (*Lanius ludovicianus*), Brown Thrashers (*Toxostoma rufum*), Blue Jays (*Cyanocitta cristata*), and other birds of the hammocks.

In the 1880's, the landscape was still relatively undisturbed; only 5 percent of Alachua County's land area had been developed for farms, towns, roads, and railroads (Webber 1883). Pearson (1891) wrote how it was possible to wander through the forests without seeing a single person or cultivated field. This evidence indicates that kestrels did nest in some of the old-growth associations. However, his nest site descriptions

and comments in the literature are too vague to compare the frequency of nests in the old-growth sandhills and pure Longleaf Pine stands with the frequency of nests in agricultural areas.

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FORAGING BEHAVIOR OF SOUTHEASTERN AMERICAN KESTRELS IN RELATION TO HABITAT USE

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Abstract: The sandhill community, particularly the pine/oak woodland habitat, provided high quality foraging sites for the southeastern American Kestrel (*Falco sparverius paulus*). Lower attack rates, higher capture success, and a greater incidence of vertebrate prey in the diet of kestrels were observed in this community than in the agricultural/mixed hardwoods community in north-central Florida. Within the sandhill community, use of pine/oak woodlands increased during breeding while use of other habitats decreased. This corresponded with increased capture of lizards. Though invertebrate prey comprised 97% of the diet by frequency in all areas, it was only 51% of the biomass consumed.

Foraging behavior of American Kestrels (*Falco sparverius*) appears closely tied to both vegetation structure and composition (Collopy 1975, Balgooyen 1976, Bildstein 1978, Mills 1979, Farquhar 1981). Accordingly, observations of the foraging behavior of the southeastern American Kestrel (*F. s. paulus*) were used to evaluate specific habitat requirements of this subspecies in north-central Florida. The southeastern subspecies occurs primarily in the sandhill community and secondarily in the agriculture/mixed hardwoods community (Bohall 1984). Seasonal and sex-specific data on foraging behavior may provide insight into the distribution of this subspecies within these 2 communities. The objectives of this study were to quantify seasonal or sex-specific differences in foraging behavior and to determine if the foraging behavior of kestrels differed in the 2 communities.

STUDY AREA AND METHODS

Behavioral observations of resident kestrel pairs were made in the mixed hardwoods community of west-central Alachua County (study area 1) and the sandhill community of east-central Levy County, Florida (study areas 2 and 3). See Bohall (1984) for specific locations of study areas.

In the mixed hardwoods community, scattered natural hardwood stands remain on deep, well-drained, fairly rich sandy soils, and are readily identified by the dense stands of shade-tolerant hardwoods and few pines. Since most of the natural hardwood areas have been harvested and converted to pasture and crop fields, the major component of this community currently is agricultural areas and hereafter will be referred to as the agriculture/mixed hardwoods community. Pine/oak woodland habitat is the major component of the sandhill community. Longleaf Pines (*Pinus palustris*) form a scattered overstory in mature natural stands, and xeric oaks, particularly Turkey Oak (*Quercus laevis*), are small understory trees. Pine harvesting and fire suppression however, have produced homogeneous stands of Turkey Oak in many areas. Extensive areas have been cleared and converted to improved pasture, pine plantations or intensive agriculture.

Study area 1 included 204 ha, of which improved pasture comprised 93%, 2% was settled, and 5% was mixed hardwood forest and wooded fencerows. Study area 2 (164 ha) consisted of 84% agricultural land, 5% open with scattered pines, and 11% pine/oak woodland habitat. Study area 3 (136 ha) included 50% improved pasture and 50% open pine/oak woodland.

Three pairs of resident kestrels (see Bohall 1984 for descriptions of *F. s. paulus*) were observed from 3 January to 29 June 1983 with wide-angle 7X binoculars and a 20-45X spotting scope. Half-day observations were conducted on each pair once each week, alternating between morning and afternoon for a total of 336.8 hours of observation on all kestrels.

The foraging behavior and success of individual kestrels were monitored using focal animal sampling (Altmann 1974). Data were collected on attack rates, success, prey taxa, and destination of prey (i.e., eaten or delivered to female or young). Prey items were classified to the smallest taxonomic category possible. Habitat type, activity, and perch type and location were recorded at 3-minute intervals. Kestrels were observed during the non-breeding and breeding periods. The start of the breeding period was signalled by intensive courtship feeding of the female by the male and ended after the young fledged.

The foraging behavior of kestrels was analyzed in relation to sex, plant community, and season. Attack rates (number of prey capture attempts per hour) were calculated for each day of observation and were tested for seasonal, sex-specific, and plant community differences using a Student's t-test (Winkler and Hays 1975). Chi-square contingency tests were used to evaluate differences in capture success and diet (Winkler and Hays 1975). Differences were significant at $p < 0.05$. Hunting success rates were calculated from prey capture attempts with known outcomes.

Table 1: Number of prey capture attempts and attack rates (number of prey capture attempts per hour) of *F. s. paulus* males and females in north-central Florida from 3 January to 29 June 1983.

Community/nesting phase	Male			Female			Combined		
	No. attempts	No./hr	SE	No. attempts	No./hr	SE	No. attempts	No./hr	SE
Sandhill									
Non-breeding	347	8.3	1.87	415	7.4	0.73	762	7.8	0.46
Breeding	275	6.4	0.95	167	4.4	0.88	442	4.6	0.69
Agriculture/mixed hardwoods									
Non-breeding	127	5.6	0.82	127	5.6	1.50	254	5.6	0.88
Breeding	350	7.3	0.70	212	6.7	1.27	562	7.0	0.71
Both habitats									
Non-breeding	474	7.5	0.49	542	6.8	0.70	1016	7.1	0.44
Breeding	625	6.8	0.62	379	4.5	0.79	1004	5.6	0.51

Table 2: Number of prey capture attempts of known outcome and percent capture success (number of successful prey capture attempts divided by number of total attempts) of *F. s. paulus* males and females in north-central Florida from 3 January to 29 June 1983.

Community/Nesting phase	Male		Female		Combined	
	n	%	n	%	n	%
Sandhill						
Non-breeding ^a	267	70.4 ^b	342	77.8	609	74.5
Breeding	241	80.5	139	74.8	380	78.4
Agricultural/mixed hardwoods						
Non-breeding	111	74.8	105	75.2	216	75.0
Breeding	274	71.9	148	65.5	422	69.7
Combined						
Non-breeding	378	71.7	447	77.2 ^b	825	74.7
Breeding	515	75.9	287	70.0	802	73.8

^a Male and female capture success rates significantly different, chi-square contingency test ($P < 0.05$).

^b Non-breeding and breeding season significantly different, chi-square contingency test ($P < 0.05$).

RESULTS

During the non-breeding period, males had higher attack rates in the sandhill community than in the agriculture/mixed hardwoods community ($t = 2.92$, $df = 27$, $p < 0.01$; Table 1), although success rates of males were similar in the 2 communities (Table 2). Breeding males had similar attack rates in the 2 communities ($t = -0.74$, $df = 43$, $p > 0.10$), but were more successful at capturing prey in the sandhill community (80.5%) than in the agriculture/mixed hardwoods community (71.9%; $\chi^2 = 5.19$, $p < 0.025$).

Success rates of females in the 2 communities were similar during both the non-breeding and breeding periods ($p > 0.05$; Table 2). Female attack rates during the non-breeding period also were similar between communities ($t = 1.20$, $df = 31$, $p > 0.20$); however, during the breeding period, females in the agriculture/mixed hardwoods community had higher attack rates than those in the sandhill community ($t = -2.59$, $df = 41$, $p < 0.005$; Table 1).

Although both male and female kestrels captured principally invertebrate prey (94.8% and 99.6% respectively), males captured relatively more vertebrates, primarily lizards (*Lacertilia*), than did females ($\chi^2 = 19.50$, $p < 0.001$). Of the 32 vertebrate items captured by males, 94% were captured during the breeding period.

Table 3: Number and percentages of prey captured by *F. s. paulus* in the agriculture/mixed hardwoods and sandhill communities of north-central Florida from 3 January to 29 June 1983.

Prey	Agriculture/mixed hardwoods				Sandhill			
	Male n	%	Female n	%	Male n	%	Female n	%
Invertebrates								
Grasshoppers (Orthoptera)	12	4.2	15	8.3	27	8.1	21	7.5
Worms (Annelida)	1	0.4	0	0.0	10	3.0	6	2.1
Dragonflies (Odonata)	3	1.1	0	0.0	7	2.1	0	0.0
Unknown	261	91.9	165	91.7	263	79.2	251	89.6
Subtotal	277	97.5	180	100.0	307	92.5	278	99.3
Vertebrates								
Lizards (Lacertilia)	6	2.1	0	0.0	22	6.6	1	0.4
Frogs (Anura)	0	0.0	0	0.0	3	0.9	1	0.4
Passerines (Passeriformes)	1	0.4	0	0.0	0	0.0	0	0.0
Subtotal	7	2.5	0	0.0	25	7.5	2	0.7
Total	284	100.0	180	100.0	332	100.0	280	100.0

In both communities males captured relatively more vertebrate prey than did females (agriculture/mixed hardwoods: $\chi^2 = 4.50, p < 0.05$; sandhill: $\chi^2 = 16.73, p < 0.001$; Table 3). Males in the sandhill community captured more vertebrate prey than those in the agriculture/mixed hardwoods community ($\chi^2 = 7.79, p < 0.01$).

In the sandhill community, kestrels hunted primarily in the open pasture habitat (Table 4); semi-open pine/oak woodlands also were used occasionally for foraging. The relative numbers of capture attempts kestrels made in these 2 habitats were used as an index of habitat use and were similar for males and females during both the breeding and non-breeding seasons ($p > 0.05$; Table 4). Combining the data from both sexes showed that kestrels increased the relative number of capture attempts in the pine/oak woodlands from 1.3% during the non-breeding season to 10.8% during the breeding season ($\chi^2 = 55.06, p < 0.001$). This clearly indicates that kestrels increase their hunting activity in this habitat type during the breeding season.

DISCUSSION

In Florida, small mammal populations are depauperate (Layne 1974), while herptile populations are extremely abundant (Kiester 1971). Thus, it is not surprising that

Table 4: Number and percentages of prey capture attempts made by 2 pairs of *F. s. paulus* in the pasture and pine/oak woodland habitats of the sandhill community in north-central Florida from 3 January to 29 June 1983.

Nesting Phase/Habitat	Male		Female		Combined	
	n	%	n	%	n	%
Non-breeding						
Pasture	347	98.9	406	98.5	753	98.7
Pine/oak woodland	4	1.1	6	1.5	10	1.3
Breeding						
Pasture	251	90.0	147	88.0	398	89.2
Pine/oak woodland	28	10.0	20	12.0	48	10.8

lizards are such an important component of the kestrel diet in Florida. Similarly, Cruz (1976) in Jamaica and Jenkins (1970) in Costa Rica found a high incidence of herptiles in the diet of kestrels. Small mammals are the predominant prey item in more temperate regions (Heintzelman 1964, Smith et al. 1972, Sparrowe 1972, Collopy 1973, Mills 1975, Craig and Trost 1979).

The diet of breeding pairs in Florida reflects the greater prey diversity and abundance in the sandhill community than in the agriculture/mixed hardwoods community. The dry pine/oak woodlands harbor an abundant lizard fauna (Florida Game and Fresh Water Fish Commission 1976) that tends to be active diurnally and consequently, vulnerable to kestrels. Kestrels foraging in this community captured 3 times more vertebrate prey, primarily lizards, than those foraging in the agriculture/mixed hardwoods community. This results in a large difference in the percent biomass of vertebrates in the diet. Precise calculations of the biomass captured by the pairs we observed were not possible because much of the prey was unidentified. However, an approximation of prey biomass captured was made using mean live weights of 0.31 g/individual for invertebrates (Koplin et al. 1980) and 6.5 g/individual for lizards, the average weight for 4 common species in Florida (Turner et al. 1969, Kitchell and Windell 1972). The percent frequency of vertebrates in the diet averaged 1.5% in the agriculture/mixed hardwoods community and 4.4% in the sandhill community. The percent biomass represented by these vertebrate prey items was 24% in the agriculture/mixed hardwoods community and 49% in the sandhill community. If only the prey of males is considered, the difference in vertebrate biomass captured is even greater: 35% in the agriculture/mixed hardwoods community and 63% in the sandhill community. By capturing more vertebrate prey, kestrels increase the energy gained per attempt for approximately the same amount of effort. Kestrels foraging in the agriculture/mixed hardwoods community also captured considerably less prey per unit time than those in the sandhill community (1.7 g/hr vs 2.7 g/hr, respectively). For males only, these values are 2.1 g/hr and 4.6 g/hr, respectively.

Lower capture success rates and less vertebrate prey in the diet may reflect lower prey diversity and abundance in agricultural areas due to the homogeneous nature of the habitat. Habitat diversity (i.e., strata of vegetation) resulted in greater herptile species diversity and abundance in a slash pine plantation as opposed to a meadow (White 1983). Similarly, insect species diversity and abundance increases with habitat diversity (Carpenter 1935, Lewis 1969, Whittaker 1970). Furthermore, seasonal changes in habitat structure are often drastic in agricultural fields, and may restrict the type of prey available. Shrubbs (1980) observed that a very low percentage of the total prey captured by Eurasian Kestrels (*F. tinnunculus*) was taken from permanent pasture habitat. He also observed a greater number of prey captured in both newly sown cereal crop fields and stubble fields than in fields with standing cereal crops (see also Bildstein 1978).

The number of foraging attempts by females during courtship and incubation also may reflect the quality of the foraging habitat within each community. The attack rate in the agriculture/mixed hardwoods community (1.61 attacks/hour) was higher than that in the sandhill community (0.91/hour). This difference is not statistically significant ($p < 0.05$; Bohall 1984), but suggests that the female in the agriculture/mixed hardwoods community had to supplement the amount of prey supplied by the male. Rudolph (1982) observed a breeding pair in California on a lower quality territory in which the female spent 18% of her time hunting during courtship and incubation and concluded that this strategy kept the energy expenditure for the pair within the normal limits of pairs on better territories. Perhaps somewhat lower habitat quality in the agriculture/mixed hardwoods community forced this pair to adopt a similar foraging strategy.

Lower attack rates and high success rates of males during breeding, particularly during the brood-rearing phase, coincided with the increased capture of lizards. Lizards increase their activity in spring due to warmer temperatures and the onset of breeding (White 1983) and, are probably more vulnerable to kestrels then. Male kestrels readily exploited this seasonally abundant food source. Other raptors similarly shift their patterns of exploitation to areas of high prey density (Lack 1946, Craighead and Craighead 1956, Phelan and Robertson 1978).

Male kestrels may increase their foraging efficiency by switching to larger, high-energy prey during the breeding season when demand for food is greatest. This pattern occurred in both communities, but kestrels in the agriculture/mixed hardwoods community continued to pounce at higher rates than in the sandhill community because of their greater dependence on invertebrate prey.

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HUNTING BEHAVIOR OF EURASIAN (*Falco tinnunculus*) AND AMERICAN KESTRELS (*F. sparverius*): A REVIEW

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Abstract: Eurasian and American Kestrels are versatile, opportunistic hunters that feed on a number of invertebrate and small vertebrate prey. Both species often cache their vertebrate prey for later consumption. The hunting behavior of both species is typical of most kestrels in that they hunt mainly from elevated perches or stationary hovering positions and take most of their prey on or near the ground. In both species, hovering is more likely during periods of moderate wind. Both species hawk insects in flight, hunt for birds while coursing in an accipitrine fashion, and hunt on the ground for insects and earthworms. Pouncing rates and hunting success vary significantly as a function of age, hunting methods, and diet. For example, hovering kestrels pounce more frequently, are less successful on a per-pounce basis, and tend to take more small mammal prey than do perch-hunting individuals. American Kestrels, but possibly not Eurasian Kestrels, exhibit widespread sex-dependent differences in the use of habitat in winter. In both species, some individuals maintain hunting territories throughout the year, especially in winter. We discuss the hunting behavior and hunting success of kestrels in light of current ecological thought and offer suggestions for further research.

"Considering that the way in which birds of prey kill is perhaps the most spectacular and interesting aspect of their lives, it is surprising how little we really know about how it is done." (Brown 1976). Unfortunately, Leslie Brown's pronouncement is nearly as true today as it was in 1976. With few exceptions, we know little of the environmental factors affecting the hunting behavior of predatory birds. Only under certain conditions can we investigate thoroughly the predatory behavior of a species: the raptor in question must hunt in open habitats; it must be rather common and not secretive; it must not range too widely or else the observer will not be able to follow it; and it must take prey frequently enough so that the observer can witness a substantial number of capture attempts.

Fortunately, both Eurasian and American kestrels meet the above criteria. Both are widely distributed species: the Eurasian Kestrel ranges over most of the Palearctic and sub-Saharan Africa except for the Congo Basin; the American Kestrel ranges throughout most of the Americas from above the Arctic Circle to Tierra del Fuego, but is not found in the Amazon Basin. Both are often the commonest diurnal raptor present in open habitats throughout their ranges, and both are found in close association with man. The Eurasian Kestrel may be the most abundant falconiform in the world (Cade 1982). Although the American Kestrel is considerably smaller than its Old World counterpart, in general the 2 species appear to be ecological equivalents. Both are versatile, open-habitat hunters that feed opportunistically on a number of invertebrate and small vertebrate prey. Both often cache their vertebrate prey for consumption later. Their hunting behavior is typical of most kestrels in that they hunt mainly from elevated perches or stationary hovering positions and take most of their prey on or near the ground.

In this paper we summarize what is known about habitat use, hunting behavior, and hunting success in the 2 species, discuss the results in light of current ecological thought, and offer suggestions for further research. Both of us have studied the hunting

behavior of American Kestrels in several habitats: KLB in Ohio and South Carolina and MWC in California and Florida. Additional information on the hunting behavior of American Kestrels is taken from published sources. Although our use of the literature is not exhaustive, we have attempted to include all major contributions. Information on the hunting behavior of Eurasian Kestrels is limited to published sources, nearly all of which deal with European populations.

DAILY PATTERNS OF ACTIVITY

Both Eurasian and American Kestrels are widely distributed raptors whose daily routines vary in accordance with local environmental conditions (e.g., Collopy 1975, Balgooyen 1976, Brown 1976, Cade 1982). At least in winter, both species spend most of their day sitting on exposed perches (Table 1). A number of researchers have observed that kestrels hover-hunt more in moderate winds than in either calm or especially windy periods, soar more on warm sunny days, and fly less in rain and fog (e.g., Bildstein 1978, Rijnsdorp et al. 1981, Village 1983). Some researchers have attempted to gauge whether perched kestrels were hunting or were engaged in other activities. Although it sometimes is possible to determine the intent of a perched kestrel, it often is difficult to do so (cf. Village 1983). As a result, the utility of these data is questionable. For example, Collopy (1975) estimated that wintering female kestrels searched for prey 87% of the time they were perched, while Meyer (1980) estimated that wintering female kestrels searched for prey only 38% of the time. Although a real difference in hunting activity may have existed between the kestrels observed by Collopy and Meyer, at least part of the difference was likely the result of observer bias. Even without observer bias, there are other complications associated with interpreting the motivation of a perched raptor. Although certain postures and activities may indeed signal the hunting intent of a perched raptor (Hamerstrom 1956), even apparently nesting raptors attempt to capture especially vulnerable prey (K. Bildstein pers. obs.; for a theoretical argument see Charnov 1976). Because of this complication, as well as expected inter-observer differences in assigning intent, we strongly recommend that when researchers split perch time into hunting and non-hunting components they also present the total amount of time non-feeding kestrels were observed perched on exposed perches. In this way data can be made comparable with results presented by other researchers.

When prey are uniformly available throughout the day, and weather is not severe, both Eurasian and American Kestrels show little diurnal variation in hunting activity, although at times American Kestrels are less active early in the morning (Tinbergen 1940, Roest 1957, Collopy 1975, Balgooyen 1976, Bildstein 1978, Village 1983). In arid environments American Kestrels restrict their activities to morning and late afternoon in summer, but hunt throughout the day in winter (Bartholomew and Cade 1957). The Eurasian Kestrel is at times crepuscular and has been reported to hunt by moonlight (Roberts 1946, Clegg 1966, Cramp and Simmons 1980). Nocturnal hunting in American Kestrels is unreported, however D. M. Bird (unpubl. data) has frequently observed this species hawking large insects in a well-lit sports stadium several hours after sunset. Females wintering in California hunted less frequently at dusk than at other times (Collopy 1975), but birds wintering in Ohio were very active at this time (Bildstein 1978). Both species store uneaten portions of their vertebrate food throughout the day, but tend to retrieve their prey more frequently in late afternoon and early evening (Collopy 1975, Rijnsdorp et al. 1981). Rijnsdorp et al. (1981) suggested that this pattern of caching, which is especially prevalent during cold weather, enables kestrels to maintain high rates of capture, uninterrupted by sluggish behavior following excessive feeding, at times when prey are most available. The pattern also increases the opportunity of a late afternoon

Table 1: Daily activity of Eurasian and American Kestrels.

Species	Sex	% of daylight hours		% of hunting time			Location/time of year (months of study)	References
		in flight	perched on an exposed perch ^a	perch hunting	hover hunting	aerial hunting		
<i>F. tinnunculus</i>	M,F	16	<<84 ^b	<71	>26	3	Netherlands/ all year (26)	(Rijnsdorp, et al. 1981)
	M,F	48	<52	>45	<55	0	Scotland/ Oct.-July (30)	(Village 1983)
	M,F	-	-	50	50	<1	Scotland/ 15 Apr.-14 Oct.(24)	(Pettifor 1983)
	M,F	-	-	85	15	<1	15 Oct.-14 Apr.(24)	
<i>F. sparverius</i>	M,F	>12	<88	75	20	5	California/ Feb.-July (5)	(Rudolf 1982)
	M	5	<91	98	1	<1	California/ Nov.-Feb. (5)	(Berdan 1976)
	F	6	<93	93	4	3	California/ Oct.-Apr. (14)	(Collopy 1975)
	M	5	<92	>85	>1	<14	California/ Oct.-Feb. (10)	(Meyer 1980)
	F	7	<89	>83	<2	<16		
	M,F	>12	<88	<88	>8	>4	Ohio/ Nov.-Feb. (14)	(Bildstein 1978)
	M,F	-	-	95	5	<<1	Texas/ Oct.-Mar. (5)	(Farquhar 1981)

^a Does not include time spent feeding, caching and retrieving prey.^b For a variety of reasons some percentages are over- or under-estimates.

meal in advance of a cold night (Collopy 1977, Rijnsdorp et al. 1981).

When prey availability varies throughout the day, the hunting activity of kestrels fluctuates accordingly. For example, kestrels wintering in California increased their attack rate in the middle of the day as temperatures increased and insects became more available (Collopy 1975, Meyer 1980), and in Holland, kestrels hunted most intensively during those periods of the day when voles were most active and hunting success was highest (Rijnsdorp et al. 1981). In the latter study, Daan (1982) calculated that 2 birds reduced their daily energetic requirements by about 4% as a result of closely tracking the activity periods of voles. Rijnsdorp et al. (1981) were able to modify the daily pattern of an individual kestrel by offering it prey at a certain location during a specific time of day; the kestrel responded by shifting its period of hunting activity and site selection to put it in the "right" place at the "right" time on subsequent days. This experiment illustrates the value of tracking the behavior of individual birds; although data collected on a group of birds inhabiting an area might fail to show a systematic pattern in temporal activity, individual birds might in fact be hunting with considerable temporal periodicity, but not in synchrony with one another.

HABITAT USE

With the exception of tundra, taiga, barren mountains, and some deserts, both species hunt in natural and modified open habitats throughout their range wherever there are adequate prey, and where nesting and roosting sites are available (e.g., Cramp et al. 1980, Cade 1982). Both occur in wetlands and mesic areas. The American Kestrel also inhabits cool deserts (Craig 1978). In Africa, the Eurasian Kestrel "occurs in mountainous terrain and adjacent areas", as well as portions of the Namib Desert (Steyn 1982).

Despite the wide range of habitats used, most studies of kestrel hunting behavior have been in areas dominated by agriculture. These studies indicate that kestrels tend to avoid hunting over tall, dense vegetation, apparently because it hinders hunting efficiency by making prey harder to see, more difficult to capture once spotted, or both (Cavé 1968, Sparrowe 1972, Balgooyen 1976). For example, Mills (1979) reported that kestrels feeding on grasshoppers in Arizona hunted only in short vegetation even though the insects were more common in tall grass. Shrubbs (1980) noted that kestrels hunting over English farmland were concentrated in clover pastures and generally absent from cereal crops, except early in the season when plants were small, and late in the season following harvest. In an Ohio study site dominated by small farms, kestrels hunted over plowed fields and grazed areas disproportionately more than over fallow fields (Bildstein 1978). In the latter study they also used smaller fields than did Rough-legged Hawks (*Buteo lagopus*) and Northern Harriers (*Circus cyaneus*), possibly because they perch-hunted more than either of these species, and smaller fields with higher ratios of field border to field area provided them with more perching sites.

Both species of kestrels concentrate along roadside edges and railway rights-of-way where they hunt from utility lines and posts. In North America, kestrels are common along the U.S. Interstate Highway System where they hover-hunt over closely mowed median strips and nest in tubular road-sign supports (K. Bildstein pers. obs.). Both species also hunt near farm buildings, possibly because the buildings provide roosting sites or because such areas are avoided by larger raptors (Mills 1975, Bildstein 1978, Shrubbs 1980). Both species sometimes hunt mice and House Sparrows (*Passer domesticus*) in open areas in cities (Bent 1938, Cramp et al. 1980). Although kestrels are not found in dense forests, they do hunt in semi-open habitats located in pine flatwoods, and in coconut and citrus groves (Bent 1938, Cruz 1976, Layne 1980).

Female American Kestrels, but apparently not female Eurasian Kestrels (Newton et al. 1982), hunt in more open habitats than do males (Koplin 1973, Stinson et al. 1981, Layne 1982); and in both species, females winter further south than do males (Layne 1982, A. Village pers. comm.). Why this is so remains unclear. The latitudinal gradient may simply reflect greater breeding site tenacity by males in harsh northern climates (A. Village pers. comm.). With regard to the differences in habitat use, several researchers have suggested the possibility of female dominance (Mills 1976, Stinson et al. 1981). Presumably, open habitats are preferred and dominant females are better able to secure them. Support for the notion of female dominance comes from several sources. Cade (1955) noted that free-ranging females attacked tethered males in their hunting territories at a higher rate than males attacked tethered females. Meyer (1980) reported that the territories of wintering females were more than twice as large as those of wintering males, and that female territories had higher densities of vertebrates. It is not known if open habitats actually are preferred by either males or females. Perch sites are fewer in open habitats and hover-hunting is more common there (Stinson et al. 1981), and it may be that kestrels hunting in open habitats expend more energy catching prey than do those in other habitats (Meyer 1980).

If dominance is involved in the establishment of sex-related differences in habitat use, it will be necessary to consider the complicating possibility of age and sex. For example, adult females might dominate all other age and sex classes, with adult males dominating juveniles of both sexes; and juvenile females dominating juvenile males. Such a complex hierarchy would be difficult to discern without the use of individually marked birds.

Although size dimorphism is relatively slight in American Kestrels (females weigh approximately 9% more than males; Snyder and Wiley 1976), males tend to be more avivorous than females (Mills 1976, K. Bildstein pers. obs.). Males may prefer denser cover and more hilly terrain because they capture avian prey more efficiently there than in more open habitats where birds can detect their approach more easily (Bildstein 1978). Stinson et al. (1981) reported that males did not use open habitats more when the females occupying them left the area. That individuals of both sexes tend to return to the same site in subsequent winters (Tabb 1977) supports the idea of sex-specific habitat preferences (Stinson et al. 1981, T. Balgooyen pers. comm.). This may only be the result however, of a tendency for individuals to return to areas where they have had experience.

We suggest that researchers interested in explaining why male and female American Kestrels use different habitats concentrate their efforts in the following areas. First, we need to determine where the reported latitudinal gradient in sex ratio actually exists. Mills (1976) and Stinson et al. (1981) correctly noted that assessing regional latitudinal differences in kestrel sex-ratios is complicated by local habitat segregation. In light of the fact that males are more common fall migrants at several locations in North America (Broun 1949, Heintzelman and Nagy 1968, Haugh 1972), and that the existence of such a gradient might act to increase competition among members of the same sex concentrating the sexes in certain areas, previous reports of males wintering further north than females need to be verified. If these reports are substantiated, we need to initiate an examination of the factors responsible for the gradient. Myers (1981) provided a methodological framework for such a study. Second, we need to determine if female kestrels exclude males from certain habitats. This could be accomplished using several manipulative approaches: (1) Expanding Cade's (1955) experiments of territorial encroachment with tethered birds to areas where males or females are the more common sex; (2) Selectively removing males and females from their territories. If females are displacing males from certain habitats, one would predict at least momentary expansion

by neighboring males into territories vacated by females, followed by the possibility of the subsequent retraction of males to their former ranges with the arrival of a new female on the site. Removal of males in territories adjacent to females should not be followed by even a momentary expansion of females into vacated (inferior?) territories. Non-manipulative approaches might include: (1) Descriptions of how mosaics of open and semi-open habitats are filled in fall with the arrival of immigrants of both sexes. If females dominate males, one would expect intra-area movement by males as females arrive and displace them from the preferred sites. (2) An examination of the relative hunting efficiencies (i.e., prey/energy expended) of males and females in both types of habitat.

The pattern of male American Kestrels wintering in less open habitats than females is typical of other species of raptors that exhibit sex-specific differences in habitat use (Bildstein 1978, Newton 1979). As similar forces are likely responsible for habitat segregation in at least some of these species, studies of habitat use by male and female American Kestrels could provide insight into habitat segregation in other raptors.

The American Kestrel is the only member of the genus *Falco* in which juveniles exhibit as much plumage dimorphism as adults. Whether this is linked to a higher proportion of second-year American Kestrels breeding than in other *Falco*, or whether it is related to sex-specific habitat segregation in the species, merits investigation.

HUNTING BEHAVIOR

Perch site use. – Both Eurasian and American Kestrels usually hunt from exposed perches, especially utility poles and telephone lines. In spring and fall in Idaho (Craig 1978), 80% of all kestrels were perched on either utility poles or telephone lines, and in 4 winters of study in Ohio (Bildstein 1978), 60% of 833 perched kestrels used these sites. The apparent heavy use of exposed perches – especially utility lines and poles – may in part reflect the fact that kestrels are more easily seen on these perches than on trees or bushes. Kestrels also hunt from fence posts, trees, snags, buildings, rocks, and herbaceous vegetation. They are found more often on wooden than on metal fence posts. On calm days, American Kestrels almost always sit on the highest perch in the immediate vicinity (Mills 1979); they perch lower as wind speed increases. Mean perching heights range from 6 to 9 m, with females in some areas perching slightly higher than males (Balgooyen 1976, Bildstein 1978, Mills 1979, Meyer 1980). In grasslands in southern Arizona and northwestern California, kestrels perched lower as insect prey increased in abundance (Collopy 1975, Mills 1979). Kestrels prefer to hunt from stable perches, especially in periods of high winds. Mills (1979) reported that they perch on utility poles and on telephone lines near poles more frequently than on telephone lines midway between poles. Craig (1978) found that 50% of the kestrels he sighted in Idaho were perched on utility poles while only 30% were perched on telephone lines. In a presumably less windy site in Ohio, kestrels perched 5 times as often on telephone lines than on utility poles (Bildstein 1978).

In areas where suitable perches are abundant, American Kestrels perch-hunt almost exclusively (Collopy 1975, Mills 1979). In 2 studies in California for example, 97% of a total of 1,289 captures were initiated from perches (Balgooyen 1976, Berdan 1976).

Eurasian Kestrels fly up to 300 m from their perch to take aerial insects (Shrubb 1982). Balgooyen (1976) found that American Kestrels make capture attempts up to 275 m from their perch; however most capture attempts occur within 50 m of the perch (Balgooyen 1976, Mills 1979, Meyer 1980, Rudolph 1983). Although Balgooyen (1976) failed to detect any change in strike distance with perching height, Mills (1979) reported a positive correlation between the 2 factors.

In Southern England, Shrubbs (1982) noted that kestrel territories characteristically possessed "favored perches overlooking good hunting sites." According to Craighead and Craighead (1956), one male kestrel was seen "in the same spot on 4 of 10 winter censuses and observed day after day to hunt from the same perch during an entire day." But even though kestrels sometimes have preferred perch sites, individuals of both species move quite frequently while perch-hunting. Shrubbs (1982) recorded that an average perching-bout lasts 8 min and is followed by movements of several hundred meters. In southern Arizona, where both bout duration and distance moved were positively correlated with perch height, the duration of a perching-bout averaged less than 3 min, and inter-perch distances averaged less than 54 m (Mills 1979). Collopy (1975) and Rudolph (1982) reported similarly brief durations for perching-bouts.

The extent to which individual kestrels vary in their tendency to hunt from a perch rather than while on the wing is unknown. Certainly, external factors such as wind speed (see section on Hover-hunting) and perch-site availability influence a kestrel's choice of hunting method, but we suggest that the developmental history of the individual also may play a role. For example, kestrels that learn to hunt in expansive habitats with few perches may tend to hunt more from the air, while those that learn to hunt areas with ample perch sites develop their perch-hunting skills more fully and hence tend to hunt more from perches as adults. Although this is a difficult question to study, we recommend that interested investigators start by determining the extent to which individual kestrels vary in their use of perch- and hover-hunting. For example, recent studies of wing-tagged Eurasian Kestrels in Britain revealed that individual birds tend to hover-hunt more during the breeding season than at other times (Pettifor 1983, Village 1983). Future studies might include observations of several kestrels hunting in the same location. For example, one could collect data on one individual, remove it, and collect data on its replacement. If such a study revealed considerable variation in the use of various hunting techniques, the next step would be to see if the differences were linked to habitat differences during development. To date, most observations of hunting behavior in raptors have concentrated on determining species- or sex-typical patterns; few have examined the extent of behavioral flexibility within species. The abundance and observability of kestrels, coupled with the fact that they can be raised easily in captivity and induced to breed in nest boxes, make them excellent candidates for studies aimed at determining the extent to which the environment influences the development of behavioral phenotypes. At least one such study on nest-type choice in captive American Kestrels has been done (Shutt and Bird 1985).

Hover-hunting. - We use the term hover-hunting as it has been used by most of the authors we cite, in the broad sense to include both flapping (true hovering) and non-flapping flight (still soaring) in which the kestrel maintains a zero ground speed, and not in the more restricted aerodynamic sense of powered flight in still air with zero ground speed. Hovering is more common in areas where tall perches are not available. American Kestrels rarely hover-hunt within 40 m of an adequate perch (Collopy 1975, Balgooyen 1976, Mills 1979); they hover-hunt more in hilly areas where up-drafts are common. Both sexes of Eurasian Kestrels appear to hunt from hovers with equal frequency (Shrubbs 1982). In the American Kestrel the situation is confounded by sex-dependent differences in habitat use. Several authors (Meyer 1980, Farquhar 1981, Stinson et al. 1981) noted that females tended to hover-hunt more than males, and suggested that the difference was the result of females using more open habitats, but others (Bildstein 1978, Mills 1979) found that males tended to hover more than females. Clearly, a study designed to test for sex-related differences in hover-hunting behavior is in order. Such a study might include paired comparisons of male and female kestrels whose territories have relatively

similar numbers and distributions of suitable perch sites or observations of pairs that overwinter on their breeding territory.

American Kestrels hunting over farmland in Ohio hover-hunted over fallow fields more frequently than over other vegetation types (Bildstein 1976); Eurasian Kestrels hunting over farmland in southern England hover-hunted over all types of vegetation (Shrubb 1982).

Both species hover at from 9 to 25 m with a mean height of about 12 m (Roest 1957, Balgooyen 1976, Bildstein 1978, Mills 1979, Shrubb 1982). Kestrels hover at lower heights as wind velocity increases, and at greater heights as prey availability declines (Mills 1979, Shrubb 1982). The latter apparently reflects an attempt by kestrels to increase the area searched as prey become harder to find.

Almost every kestrel researcher has remarked on the tendency of birds to hover more in moderate winds (10-30 km/h) than in lighter or heavier winds; kestrels rarely hover in still air. Mills (1979) suggested that kestrels hover most when wind speed approaches the velocity of minimum power, the speed at which flapping flight is least costly per unit time. Rudolph (1982) and Village (1983) suggested that male kestrels hover more during the breeding season because they are supporting a greater biomass (i.e., their mate and offspring).

Although kestrels sometimes hover for more than a minute at a time (Brown and Amadon 1968), the mean duration of individual hovers is much less: 16-18 sec in American Kestrels (Bildstein 1978, Mills 1979) and 26 sec in Eurasian Kestrels (Shrubb 1982). When hunting for small mammals, kestrels frequently interrupt their descent with several hovers as they close in on sighted prey (Roest 1957, Bildstein 1978, Mills 1979, Cramp and Simmons 1980, Shrubb 1982). Most of these occasions are followed by a pounce (Mills 1979). At least one species of microtine rodent moves about more when hawk-like silhouettes are stationary overhead than when the silhouettes are moving (Bildstein and Althoff 1978). Thus, it may be that within-descent hovers (i.e., stationary periods) act to induce movement in previously sighted small mammals, thereby increasing their vulnerability to hover-hunting kestrels. In Arizona, kestrels pounced from 29% of 430 hovers (Mills 1979), in England from 11% of 567 hovers (Shrubb 1982; see also Brown and Amadon 1968). Kestrels usually dive head-first at small mammals and feet-first at insects (Roest 1957).

A number of researchers have discussed the relative advantages of hover-hunting versus perch-hunting (i.e., Mills 1979, Rudolph 1982; see section on Hunting success). Most agree that hover-hunting enables kestrels to exploit areas with few if any perches. As the energetic cost of hover-hunting is correlated with wind speed, use of this technique by kestrels is restricted by local atmospheric conditions. Whether or not kestrels are less common in relatively windless areas where hovering is energetically more costly, is unknown.

Flight-huntings. - In addition to hunting for prey from perches and from hovers, kestrels hunt while cruising in flapping and soaring flight. In California, kestrels use this method in warm weather to hunt for insects (Rudolph 1982, Collopy and Koplin 1983). Wintering American Kestrels (Bildstein 1978) and breeding Eurasian Kestrels (A. Village pers. comm.) flight-hunt for passerines over farmland; and in coastal areas, both species flight-hunt for shorebirds (Page and Whitacre 1975, Rijnsdorp et al. 1981). Flight-hunting is also used at the communal roosts of avian and chiropteran prey, where kestrels take incoming and outgoing individuals (Spencer 1946, Cruz 1976), as well as along fire lines of grass fires (Brown and Amadon 1968).

Less frequently used hunting methods. - In addition to the types of hunting described above, Eurasian and American Kestrels sometimes walk about on the ground searching

for insects and earthworms (Balgooyen 1976, Berdan 1976, Cramp and Simmons 1980, Shrub 1980), and American Kestrels take insects from the trunks of trees (Balgooyen 1976). In North America, kestrels pluck nestling and recently fledged Bank Swallows (*Riparia riparia*) and Cliff Swallows (*Petrochelidon pyrrhonota*) from their nests (Brown and Amadon 1968, Freer 1973, Windsor and Emlen 1975), and Eastern Bluebirds (*Sialia sialis*) and House Sparrows from nestboxes (Steffen 1981). Individual kestrels may learn this hunting technique when they chase recently fledged young back into their nestboxes. Kestrels also catch prey disturbed by the movements of cattle and farm implements (Brown 1976, Bildstein 1978, Shrub 1980, Rudolph 1982).

HUNTING TERRITORIES

Both species appear to be territorial in the winter, at least when food is scarce (Cade 1955, Cavé 1968, Collopy 1975, Mills 1975, Cramp and Simmons 1980). In California in winter, females maintained larger territories in more open habitats than did males (Meyer 1980). During the breeding season, Eurasian Kestrels defend a small area around the nest (e.g., 25-30 m radius); they usually nest solitarily but sometimes only a few meters apart (Brown and Amadon 1968, Cavé 1968). Territorial behavior is less pronounced during the breeding season when Eurasian Kestrels do not appear to defend hunting areas (Cavé 1968, Village 1982). The average size of territories of breeding American Kestrels can vary greatly depending on habitat and prey base. In California (Balgooyen 1976) and Michigan (Craighead and Craighead 1956), mean territory size averaged 109 and 129 hectares, respectively; in Florida (Hoffman 1983), kestrels occupied territories of approximately 50 hectares.

HUNTING SUCCESS

A number of studies indicate that hunting success of kestrels varies both with prey types taken and with hunting techniques employed, and that success may vary with age and sex as well. But before we detail the results of these studies we first need to define hunting success. Most researchers have defined hunting success as the number of captures per hunting attempt (Rudebeck 1950, Kruuk 1972, Curio 1976). Unfortunately, a problem arises when we apply this definition to kestrels, i.e. what does the term hunting attempt refer to? Is a perched kestrel engaged in a new hunting attempt each time it perches again, or turns its head, or pounces or swoops? Similarly, is a hover-hunting kestrel engaged in a new hunting attempt each time it hovers, or initiates a descent, or only when it pounces? In this review we follow the convention used by most kestrel researchers and define a hunting attempt as an effort by a kestrel to catch a specific prey item (i.e., a pounce or a strike (Bildstein 1978)). As aerial attempts at prey capture lack definite pounces, reports of the hunting success of kestrels hawking insects and chasing birds do not fit nicely into our conventional scheme. Although we report hunting success rates for aerial-hunting kestrels, as well as for perch- and hover-hunting individuals, we caution the reader that the former are not readily comparable with the latter. Indeed, because of differences in the way observers establish hunting attempts for aerial-hunting kestrels, these rates may not be comparable even among themselves.

The hunting success of kestrels varies with hunting technique (Tables 2 and 3). In general, hover-hunting kestrels catch fewer prey per pounce than do perch-hunting kestrels, but hovering birds pounce more frequently than perched birds, and they capture more prey on an hourly basis (Table 2). We suggest that one or more of 4 factors are responsible for these differences. First, kestrels may pounce more frequently from hovers because hovering provides more strike opportunities than perching. Second, kestrels may

Table 2: Pouncing rates, pouncing success, and capture rates of perch-hunting and hover-hunting Eurasian and American kestrels.

Location (season)	N ^a	Pounces per hour	Percent successful pounces	Captures per hour	References
<i>F. tinnunculus</i>					
England (all year)	63	-/16 ^b	-/52	4/8	(Shrubb 1982)
Netherlands (all year)	-	-/-	-/36	0.2/3	(Rijnsdorp et al. 1981)
Scotland (all year)	-	3/8	56/47	1/4	(Village 1983)
<i>F. sparverius</i>					
California (non-breeding)	827	-/-	57/31	-/-	(Berdan 1976)
California (breeding)	<874	17/45	56/57	11/26	(Rudolph 1982)
California (non-breeding)	2275	-/-	77/27	7/15	(Collopy 1975)
California (non-breeding)	2544	8/-	40/36	-/-	(Meyer 1980)
California (all year)	813	13/-	70/-	9/-	(Balgooyen 1976)
Arizona (not given)	249	-/50	57/51 ^c	3/17	(Mills 1979)
Ohio (non-breeding)	128	-/75	63/30	-/18	(Bildstein 1978)
Florida (all year)	1857	-/-	78/55	-/-	(Collopy unpubl.)
Michigan (breeding)	54	-/-	36/14	-/-	(Sparrowe 1972)

N^a = number of pounces used to calculate present successful pounces. Sample sizes used to calculate pouncing and capture rates are sometimes smaller.

^b Perch-hunting/Hover-hunting.

^c A number of pounces of unknown outcome, but probably unsuccessful, are not included.

be more likely to hover as they become increasingly food stressed. If this is so they may be more anxious to capture prey when hovering and hence more likely to pounce in marginal circumstances. Third, there are indications, at least for Eurasian Kestrels, that juveniles hover-hunt more than adults. If this is so, and if juveniles are less efficient hunters than are adults (cf. Newton et al. 1982), age-related differences in hunting behavior may be responsible for the observed difference in pouncing success. Fourth, hovering kestrels are expending energy at considerably higher rates than are perched kestrels (see Koplin et al. 1980). As pouncing from a hover does not represent as

Table 3: Hunting success of aerial-hunting Eurasian and American Kestrels.

Location (season)	Type of aerial-hunt	N ^a	Percent successful	References
<i>F. tinnunculus</i>				
England (all year)	Bird chases	87	31	(Shrubb 1982)
<i>F. sparverius</i>				
California (non-breeding)	Insect chases	14	57	(Berdan 1976)
California (non-breeding)	Mostly insect chases	582	47	(Collopy 1975)
California (non-breeding)	Bird chases	104	9	(Meyer 1980)
	Hawking insects	28	57	

N^a = number of hunting attempts.

massive an increment in instantaneous energetic expenditure as does pouncing from a perch, and as the cost of not pouncing is considerably higher for a hovering bird than for a perched bird, it seems likely that hovering kestrels pounce less selectively, and as a consequence more frequently than perched bird, because of energetic considerations. This latter possibility predicts that kestrels hovering in low winds, when the cost of hovering is high, will pounce more frequently than those hovering in higher wind, when costs are lower.

Several researchers (see Mills 1979, Rudolph 1982) have attempted to compare the relative costs and benefits of hover-hunting, a high-cost, highbenefit method of hunting with perch-hunting, a low-cost, low benefit hunting method. There is general agreement that American Kestrels employ hover-hunting more frequently as wind speed increases, presumably because higher winds tip the relative cost-benefit ratios in favor of hover-hunting. On the other hand, Rudolph (1982) and Village (1983) reported that kestrels hover more when they are raising young than at other times. Both researchers suggested that this might be an attempt on the part of adults to maximize the amount of prey delivered to their young rather than an attempt to minimize the overall cost-benefit ratio of hunting. Additional factors that might affect a shift toward hover-hunting during the breeding season relate to the notion of central place foraging (Orians and Pearson 1979). Hover-hunting may enable breeding kestrels to hunt closer to their nests, thereby reducing the costs of transporting prey. Hover-hunting also may enable birds to increase the proportion of energetically profitable vertebrate prey in their diet. Another possibility is that hover-hunting may allow birds to hunt closer to the nest, thereby enhancing their ability to guard offspring. Yet another possibility, not restricted to breeding birds, is that kestrels, by hovering over areas not searched when they are perched, reduce predation pressure on these latter areas conserving prey therein for later use, possibly by their offspring. The use of the doubly labelled water technique of

assessing metabolic expenditures (Lifson and McClintock 1965, Hails and Bryant 1979), if coupled with well established falconry techniques (see Fox 1981), would offer kestrel researchers the opportunity to determine if kestrels do indeed hover-hunt only when the increased benefits of hover-hunting outweigh the increased energetic expenditures, or if kestrels hover-hunt even when it is more costly than perch-hunting.

Reports of hunting success for aerial-hunting kestrels vary considerably (Table 3). Although some of this is probably the result of the different types of prey taken, part of the variation may be the result of researcher-specific criteria for establishing the occurrence of hunting attempts. Although, as indicated, these data are not comparable with data reported for perch- and hover-hunting kestrels, it would be possible to compare rates of capture per unit time among the 3 techniques and to estimate the cost-benefit ratios of each. As aerial-hunting often is coupled with certain weather conditions (i.e., insect chases increase in warm weather as flying insects become more abundant and as updrafts form; bird chases increase during periods of snow cover when small mammals become less available), comparisons of cost-benefit ratios should be limited to observations collected at times when birds engage in all 3 hunting methods.

Hunting success also varies with prey types taken. Perch- and hover-hunting kestrels are more successful on a per-pounce basis when they hunt for insects than when they hunt for vertebrate prey (Collopy 1975, Balgooyen 1976, Village 1983); aerial-hunting kestrels are more successful when hawking insects than when chasing birds (Table 3). Recently fledged kestrels are especially dependent on insect prey as they develop their hunting skills (Shrubb 1982).

Male American Kestrels are apparently more successful on a per-pounce basis than are females (Bildstein 1978, Meyer 1980, Farquhar 1981), but despite extensive observations, Bohall (1984) found virtually no sex-related differences in hunting success among kestrels breeding and wintering in north-central Florida. As male and female American Kestrels often hunt in different habitats, reported differences in hunting success may reflect habitat and prey-base effects rather than sex-related differences in hunting ability. Clearly, more study is needed in this area.

CONCLUSIONS AND SUGGESTIONS FOR FUTURE RESEARCH

A strong case already has been made for using the American Kestrel as a model species in laboratory research (Bird 1982). A similar case can be made for using American and Eurasian kestrels as model species in field studies of hunting behavior and ecology. Both species possess a number of traits that make them especially attractive to field researchers. As this review indicates, considerable effort has been devoted to studying the hunting behavior of Eurasian and American Kestrels. Indeed, the hunting behavior of these 2 species is perhaps as well known as that of any raptor and with good reason. Free ranging individuals of both species are relatively easy to watch; both species are rather common and not secretive; both take prey frequently, so that a substantial number of capture attempts can be witnessed in a relatively brief period; and both readily accept artificial nest-boxes, enabling researchers to manipulate the density of kestrels during the breeding season, as well as affording researchers easy access to nest sites. Finally, both species exhibit sexually dimorphic plumage as well as sexual size dimorphism (American Kestrels can be sexed by plumage in their first year; Eurasian Kestrels, in their second year).

The above traits combine to make American and Eurasian Kestrels ideal candidates for ecological study including studies related to optimal foraging theory and the many hypotheses concerning the function of reversed sexual size dimorphism in raptors. Below is a list of areas that pose a number of questions we believe merit additional research:

1. *Sex-related differences in habitat use.* Although the causes and consequences of reversed sexual size dimorphism in raptors have received considerable critical attention, there has been relatively little empirical testing of the many hypothesis thus generated. We believe that a close examination of habitat segregation in male and female American Kestrels will at least reveal some of the consequences of reversed sexual size dimorphism in raptors.

Sex-related habitat segregation apparently is more common in American than in Eurasian Kestrels. Perhaps Eurasian Kestrels face greater inter-species competition for resources than do American Kestrels. We suggest that researchers on both sides of the Atlantic attempt to measure the relative intensities of intra- and inter-species competition in American and Eurasian Kestrels. This is not an easy task, but one that needs to be done if we are to understand sex-related differences in habitat use in the 2 species.

2. *Choice of hunting methods.* Kestrels appear to be ideally suited for testing optimal foraging theory, especially with regard to the question of hunting method. What are the immediate energetic costs and benefits of perch- versus hover-hunting? How well do kestrels monitor the relative benefits of each method? How often do they switch between the 2 methods? How quickly do they attain maximum capture rates after switching?

3. *Individual variation in hunting behavior.* To date, most studies of hunting behavior have averaged the behavior of individuals in certain age or sex classes, or have investigated seasonal changes in hunting behavior. Few, if any studies, have attempted to assess the effects of individual differences in hunting behavior on longevity or reproductive success. Long-term studies of individually marked kestrels could provide an understanding of the adaptive significance of hunting strategies.

4. *Development of hunting behavior.* How long does it take a kestrel to attain maximum hunting efficiency? Do those individuals that breed in their first year hunt more efficiently than do those that defer breeding until their second year? Does the presumed dependence of juvenile kestrels on insect prey affect their choice of wintering areas?

5. *Hunting success, habitat use, and nest-site selection.* To what degree does the availability of hunting habitat affect nest site selection? This question might be answered in 2 ways. First one could erect nest boxes in a number of habitat types and examine their relative use, as well as the reproductive success of birds using them. Second, one could modify the habitat surrounding nests (i.e., by erecting a series of poles for use as hunting perches) and observe the response of kestrels breeding in the area.

6. *Winter hunting territories.* At least some kestrels maintain hunting territories during the winter. Presumably they do so to keep out other kestrels that have been unable to find suitable wintering ranges of their own. What do those other kestrels do over the course of the winter? Do they finally settle in less attractive areas, or do they remain as part of a "floating population" until spring? If the former is true, one would expect that kestrels removed from their territories early in the season (October-December) would be replaced more quickly than those removed later in the season (January-March). Another question that will prove more difficult to answer is: To what extent does the possession of a winter territory affect hunting success and survivorship?

7. *Association with man.* How does the hunting behavior and success of city- and town-dwelling kestrels compare to that of more rural individuals?

8. *Inter-species comparisons.* Although Eurasian and American Kestrels are assumed by many to be ecological equivalents, we know of no field studies comparing the hunting behavior of the 2 species. Aside from the fact that American Kestrels exhibit sex-related differences in wintering habitat while Eurasian Kestrels apparently do not, our readings of accounts of the 2 species left us with the impression that Eurasian Kestrels hover-hunt

considerably more than do American Kestrels. We strongly recommend that European and North American researchers consider combining their efforts in a truly comparative study of the 2 species.

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PREY SELECTION BY KESTRELS: A REVIEW

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Abstract: Prey selection by kestrels will remain a controversial issue. Field studies tell us what the birds actually prey upon, but fail to enlighten us about selection since the availability of prey at the moment a bird selects is impossible to measure. Laboratory studies inform us about some of the details of the selection process, but it is impossible to determine whether these results can be extrapolated from the controlled confines of the laboratory to the complexity of the wild.

Field studies have shown that kestrels prey on a great variety of invertebrates and vertebrates, suggesting that the birds are opportunistic predators with little preference for any particular type of prey. However, evidence from a new field investigation indicates that individual kestrels will at least occasionally and temporarily specialize on particularly vulnerable prey species. Kestrels feed largely on insects until cold weather eliminates or reduces their availability, after which they switch to vertebrate prey. Laboratory experiments suggest that kestrels can learn to assess their probability of prey capture and that they develop long lasting preferences for particular kinds of prey (e.g., colors of mice). Laboratory experiments also suggest that there is a preference for odd prey, or prey of unusual appearance, providing that the appearance of the "prey" is within the limits of that occurring in nature. It appears reasonable to assume, at this point in our knowledge, that kestrels have a tendency to specialize on types of prey which are sufficiently and easily obtainable to provide for metabolic needs and that there also may be a contrary tendency to select odd prey.

The American Kestrel (*Falco sparverius*) is known to prey upon a great variety of animals (Fisher 1893, McAtee 1935, Heintzelman 1964, Balgooyen 1976). Invertebrates taken as prey include earthworms, spiders, centipedes, scorpions, and insects of 7 orders, including both larval and adult forms of Diptera, Lepidoptera and Coleoptera. Kestrels, (unless otherwise indicated, "kestrel" refers to the American Kestrel) also occasionally capture frogs and at least one toad has been recorded as prey. Reptiles as prey include 5 genera of lizards and at least 6 species of snakes. Over 30 species of birds are listed as prey, ranging in size from under 10 g (i.e., Bushtit (*Psaltiriparus* sp.) to well over 150 g (i.e., full-grown Northern Bobwhite (*Colinus virginianus*)). About 30 species of mammals also have been listed as prey, with a size range similar to that of avian prey: from shrews (*Soricidae*) and bats (*Vespertilionidae*, *Molossidae*) to rabbits (*Sylvilagus* sp.), wood rats (*Neotoma* sp.) and pocket gophers (*Thomomys* sp.). This list of prey, drawn largely from analyses of stomach contents, pellets, and prey brought to, or remains found in nests, strongly suggests that the kestrel is a generalist, an opportunistic predator that preys upon whatever is immediately available. There are some suggestions to the contrary. For example, Hart (1972) identified the remains of prey in 8 kestrel nest boxes after a breeding season characterized by unusually low (*Microtus*) populations. There was a considerable difference in prey composition between the nests, ranging from 40% to 96% insects, 0% to 54% birds, and <1% to 28% mammals, suggesting the possibility that individual kestrels might be preferring certain types of prey and not simply responding to relative abundance.

However, all other major field studies of the prey taken by kestrels lump data from many individuals and over considerable periods of time and thus tell us very little about

how and why an individual bird selects a prey item as well as the spectrum of choices available to it at that time. This review of prey selection in kestrels will thus concentrate on the results of experiments and those data from field studies which offer some insight into the behavioural aspects of selection.

THE LABORATORY EXPERIMENTS OF MUELLER (1968-77)

My experiments with kestrels were inspired by the observations and field experiments of Pielowski (1959, 1961). Pielowski found that Goshawks (*Accipiter gentilis*) showed a statistically significant preference for domestic pigeons (*Columba livia*) which differed in color from the majority of pigeons. He systematically collected the remains of Goshawk kills in a forest and found that domestic pigeons were an important prey item and that 60% of the pigeons killed ($N=362$) were dark colored. A survey of pigeon lofts in the nearby villages revealed that the population contained only 13% dark birds, and the Goshawks were thus selecting significantly more dark pigeons than expected ($\chi^2 = 176, p < 0.0001$). Pielowski then established a loft in a forest devoid of villages and pigeons and stocked it 86% (18) dark colored birds and 14% (3) with considerable white in the plumage. In this situation, 53% of the attacks ($N=68$) were directed at largely white birds, which differs significantly from the expected ($\chi^2 = 20.5, p < 0.0001$). The Goshawks thus seemed to prefer odd, or unusually colored pigeons. Domestic pigeons from a loft usually occur in flocks, and this raises the possibility that the Goshawks were selecting conspicuous individuals out of the flock, rather than odd individuals. The question of whether oddity actually influenced prey selection appeared impossible to resolve in the field, so I turned to the laboratory.

The kestrel was the obvious choice as a raptor for the experiments: it is small, abundant, readily obtained, easily tamed, and adapts readily to the confines of the laboratory. Albino laboratory mice were chosen as prey for several reasons: they are cheaply available, easy to handle in a laboratory environment, inbred strains are available (which greatly reduces individual variability in movement and other behaviors), and the use of tasteless food dye permits the use of color as a variable while other factors that might influence selection can be kept as constant as possible.

I present a summary of the results of my experiments in chronological order, with sufficient detail so that the reader can see how: (1) the design of the experiment influenced the results obtained, (2) the conclusions derived from one experiment led to the design of the next, and (3) the experimental design and results are relevant to prey selection as it occurs in nature. My first experiment (Mueller 1968a) was an attempt to determine whether kestrels would show selective predation in the laboratory. The experimental design was simple (Table 1): a kestrel was offered 10 mice, 9 either white or dyed gray, and 1 of the other color. In this initial experiment, all 50 trials of Series A were done first, then series B, then C, then D. The results were: 13 white mice selected in Series A, 50 in Series B, 6 in Series C, and 44 in Series D. Thus, white mice were preferred in Series A and B where they were conspicuous, but no preference for color was shown in Series C and D when white mice were inconspicuous. I interpreted these results to indicate: (1) a preference for conspicuous mice, which explains the results from Series A and B, and (2) that the kestrel established a color preference for white (conspicuous) mice in Series A and B, which then conflicted with the preference for conspicuous (gray) mice in Series C and D, resulting in no preference.

I prefer to characterize the tendency of a predator to select a given type of prey (in this case, white mice) as a specific searching image (SSI), after Tinbergen (1960). This concept was first advanced by Von Uexkull (1934) who pointed out that it is easier to find something with characteristics familiar to you. Tinbergen (1960) applied this concept to

Table 1: Design of Experiments 1 and 2 in kestrel prey selection.

Series	No. of trials	Substrate	Mice presented in each experiment		Expected total catch ^a	
			Gray	White	Gray	White
A	50	Gray	9	1	45	5
B	50	Gray	1	9	5	45
C	50	White	9	1	45	5
D	50	White	1	9	5	45

^a If there is no, or random selection.

predators seeking prey. He contended "that the birds perform a highly selective sieving operation on the visual stimuli reaching their retina". This is an apt explanation of the processes involved in prey selection by Gandalf and Thorin, two unusual birds among my 16 kestrels, in that they would occasionally approach prey indirectly. They would often land on the 10 x 10 cm pedestal occupied by a mouse next to the one they were intending to capture; this mouse was invariably of the non-preferred color (non-SSI). When the mouse sniffed at the feet of the kestrel, or otherwise made contact, the bird would take flight, obviously frightened. Less frequently, the kestrel would land on a mouse of the non-SSI color adjacent to a mouse of the SSI color and fly up in apparent fright when its "perch" moved. It is difficult to explain these observations without invoking the concept that the non-SSI mouse was not perceived as prey.

In my first experiment, I presented the 10 mice to the kestrel on a table covered with a gray or white cloth. The mice tended to huddle in a dense group, and the kestrel tended to select those that were not in the group. The kestrel also appeared to select the nearest mouse, even though distances from the kestrel were minimal on the 91 x 136 cm table. Moving mice appeared to be selected more often than immobile mice. The effect of these uncontrolled variables was to reduce the selection for oddity, because an odd mouse would exhibit a randomly occurring behavior only 10% of the time, while ordinary mice would have a 90% probability of showing the behavior. In my remaining experiments I greatly reduced the variability in movement and distance and eliminated grouping by placing the mice on 10 x 10 cm pedestals (and 15 cm high) arranged 10 cm apart on an arc of a circle of 2 m radius, with the kestrel placed at the center of the circle.

My second experiment (Mueller 1971) was designed to determine whether an SSI would be formed if the color of the substrate and the odd mouse were changed frequently and randomly. The basic experimental design was as presented in Table 1, except that the "series", or mouse and substrate combinations, occurred randomly throughout the 200 trials. Six kestrels were used in the experiment (Table 2). Two showed a significant preference for gray mice, but only when gray mice were odd. Four showed a significant preference for white, odd mice and two of these also preferred white, common mice but only when they were conspicuous (Series B). No other evidence for selection of conspicuous mice was found. My interpretation is that the SSI was the most important

Table 2: Results of Experiment 2 in kestrel prey selection: number of odd mice taken.

Kestrel	Experiment "Series"			
	A	B	C	D
Lucy	4	16 ^a	2	16 ^a
Arwen	4	16 ^a	2	21 ^a
Gimpy	25 ^a	6	21 ^a	6
Frodo	10 ^a	4	15 ^a	9
Bilbo	31 ^a	0 ^a	18 ^a	4
Gandalf	48 ^a	0 ^a	31 ^a	1

^a Departs significantly from the expected value, chi-square test, $p < 0.05$.

determinant in prey selection, but that oddity was also important. Conspicuousness was relatively unimportant. The experimental design failed to prevent the formation of an SSI and subsequent analysis of the data failed to yield a clue as to how the kestrels formed an SSI.

My third experiment (Mueller 1974a) was designed as an attempt to induce an SSI in a kestrel and then to determine its persistence as the bird was offered decreasing ratios of SSI mice. Each kestrel was offered 10 mice, all of one color for 30 trials, with the assumption that this would establish an SSI for that color (Table 3). Each kestrel was then offered 9 mice of the SSI color and 1 (odd) mouse of the other color for 50 trials. In Tests 2 through 9 the ratio of SSI mice was gradually reduced so that in Test 9 one SSI (odd) mouse and 9 mice of the other color were offered. This experimental procedure was performed 4 times with each kestrel in every possible combination of color of SSI mouse and substrate color (Table 4). Each of the 5 kestrels thus made 888 selections, and captured another 120 mice during no-choice training trials.

The most striking result of the experiment was their preference for a given color of mouse, through all or most of the 4 series (Table 5). This preference was not influenced by the experimental design, which was an attempt to manipulate the SSI. These unanticipated results could not be dealt with adequately by the analysis of variance selected for the experimental design (Mueller 1974a). I have re-examined the data several ways and present a summary of the 2 most informative analyses below. In both, I pooled the data for all 5 birds, ignoring the individual differences which were emphasized in the original paper. In the first analysis, I examined the number of individual tests in which selection was significantly different from expected (random) and which of these support or oppose the following selection hypotheses: (1) SSI, (2) Conspicuousness, (3) Color (an overall preference for a color of mouse, and (4) Uncommonness or oddity (Table 6). Each kestrel was subjected to 9 Tests in each of 4 Series, yielding 180 individual tests for the 5 kestrels. In part A of Table 6, Test 5 has been deleted because gray and white mice are equally common, yielding 160 individual tests, of which 101, or 63% differed significantly from expected. Similarly, Part B includes only Tests 1 and 9 because mice

Table 3: Experiment 3: Design for each series in kestrel prey selection.

	No. of trials	Mice presented in each trial		Expected catch ^a	
		SSI Color	Other Color	SSI Color	Other Color
Train	30	10	0	30	0
Test 1	50	9	1	45	5
Test 2	25	8	2	20	5
Test 3	18	7	3	12.6	5.4
Test 4	13	6	4	7.8	5.2
Test 5	10	5	5	5	5
Test 6	13	4	6	5.2	7.8
Test 7	18	3	7	5.4	12.6
Test 8	25	2	8	5	20
Test 9	50	1	9	5	45

^a Assuming no, or random selection.

Table 4: Experiment 3: design differences between series in kestrel prey selection.

Series	SSI ^a Color	Substrate Color	Other attributes of SSI ^a mice	
			Tests 1–4	Tests 6–9
A	White	Gray	Conspicuous	Uncommon, Conspicuous
B	Gray	Gray		Uncommon
C	Gray	White	Conspicuous	Uncommon, Conspicuous
D	White	White		Uncommon

^a Assuming that an SSI will be established by the 30 training trials.

can be odd only in these two. This yields 40 individual tests, of which 55% differ significantly from expected.

The SSI, uncommonness, and overall color preference all appear to influence selection when we include all but Test 5 in the analysis (Table 6A). Only conspicuousness is eliminated as a factor influencing selection, with about as many individual tests opposing as supporting. However, a mouse in these experiments has, simultaneously, several

Table 5: Experiment 3: individual color preferences in prey selection by captive kestrels.

Series	Kestrel				
	Gandalf	Frodo	Aragorn	Gala	Varda
A	0.97W ^a	0.72W ^a	0.67G ^a	0.88W ^a	0.98W ^a
B	0.63G ^a	0.64G ^a	0.61W ^a	0.83W ^a	0.97W ^a
C	0.51G	0.89G ^a	0.86W ^a	0.75W ^a	0.64W ^a
D	0.56G	0.57G ^a	0.91W ^a	0.72W ^a	0.64W ^a
TOTAL	0.57W ^a	0.59G ^a	0.68W ^a	0.78W ^a	0.81W ^a

^a Differs significantly from random, chi-square test $p < 0.05$.

attributes. Of the 61 individual tests in which selection for the SSI was indicated, 57 also can be interpreted as selection for overall color preference and 39 as selection for uncommonness, leaving no tests that offer unequivocal evidence for the SSI. This suggests that the SSI is not a factor in prey selection in this experiment.

This leaves uncommonness and the overall color preference; the selection shown in 64 individual tests can be attributed to either of these factors. Thus, when we consider all those tests in which the ratio of colors of mice varies from 6:4 to 9:1, the long-term color preference appears to be the most important factor influencing prey selection.

When we limit the analysis to tests 1 and 9, where the colors of mice appeared in a ratio of 9:1, it appears that oddity and the overall color preference are important; both the SSI and conspicuousness disappear as possible influences on prey selection. Of the 17 of 21 tests showing selection for a long-term color preference and oddity, 16 can be attributed to either of these factors. This suggests that oddity is slightly more important than the long-term color preference as a determinant of selection when the ratio of colors of mice is 9:1.

The long-term color preference of the kestrels can be regarded as a *long-term SSI*, one which was not influenced by experimental attempts to manipulate the SSI; indeed, my efforts to establish an SSI and change it were a complete failure. Although I cannot explain how kestrels establish a color preference, and why they change, the fact remains that kestrels do develop preferences for a given color of mouse, and I will argue that the concept of the SSI is as valid an explanation for this preference as any other.

If we need consider only type of prey (color) and frequency (the proportions of the 2 types of prey available), the data then are amenable to an analysis comparing observed values with expected values derived from ecological hypotheses of predation (Table 7, A–D). The appropriateness of each hypothesis as an explanation for the results can be appraised by examining whether or not the proportion predicted by the hypothesis for each ratio of prey types presented falls within 2 standard errors of the mean for the observed values and by the chi-square. The chi-square was calculated by the difference between observed numbers of prey types taken and those predicted by the hypothesis

Table 6: Number of individual tests which support or oppose selection hypotheses^a in kestrel prey selection.

Selection for:	No. tests supporting	No. tests opposing
A. Tests 1-4 and 6-9 ^b		
SSI	61	40
Conspicuousness	51	50
Color ^c	90	11
Uncommonness	76	25
B. Tests 1 and 9 ^d		
SSI	12	10
Conspicuousness	11	11
Color ^c	17	5
Oddity	21	1

^a Number of individual tests which show selection statistically different from expected, chi-square test, $p < 0.05$.

^b Test 5 was deleted because both colors of mice were equally common; thus, $N=160$ - the 59 which show no significant difference from expected = 101.

^c Selection for a given color of mouse, regardless of SSI, taking into account the switches in color preference shown in Table 5.

^d Tests 2-8 were deleted because odd mice occur only in Tests 1 and 9; thus, $N=40$ - the 18 which show no significant difference from expected = 22.

for each of the ratios of prey presented and then summed for all 9. The selection shown by my kestrels differs significantly from that predicted by all 4 ecological hypotheses (Table 7, A-D). Selection is not merely dependent on the frequency of availability of type of prey (Table 7, A). Although kestrels show a reasonably strong preference for white mice (62%) when white and gray mice were offered in equal numbers (5:5), this preference was not constant over all prey frequencies (Table 7, B). Selection was not a simple multiplicative function of frequency and preference (Table 7, C). The remaining ecological hypothesis, switching (Murdoch 1969), provides the worst fit to the data on any of the four (Table 7, D). The best fit of a preference and frequency dependent curve utilizes the cube root of frequency (Table 7, E). Although it is curious that the best fit to my data is provided by a frequency exponent of 0.33 (and not, e.g., 0.32 or 0.34), I do not think that this indicates some special relationship. An exponent of less than 1 increases the expected values at low frequencies and decreases the expected values at higher frequencies. The lower the value of the exponent, the greater are the effects. An exponent of 0 yields the same expected proportion at all frequencies (0.62 for Experiment 3).

A simple explanation for the results of Experiment 3 is that the kestrels strongly preferred a mixture of 0.62 white and 0.38 gray mice and that frequency of the 2 prey

Table 7: Experiment 3: comparison of proportions of white mice taken and those expected by various hypotheses in kestrel prey selection.

	Ratio of white: gray mice presented									
	9:1	8:2	7:3	6:4	5:5	4:6	3:7	2:8	1:9	
x White taken	.80	.75	.69	.66	.62	.67	.64	.60	.46	
x + Standard errors	.91	.87	.83	.80	.78	.82	.78	.74	.60	
x - Standard errors	.69	.63	.55	.52	.46	.52	.50	.46	.30	
White expected										Chi-square ^a
A. Frequency dependent, No preference	.90	.80	.70	.60	.50	.40	.30	.20	.10	2,086
B. Frequency independent, Preference at ratio 5:5	.62	.62	.62	.62	.62	.62	.62	.62	.62	296
C. Frequency dependent, Preference ^b	.94	.87	.79	.71	.62	.52	.41	.29	.15	1,524
D. Switching hypothesis ^c	.99	.96	.90	.79	.62	.42	.23	.09	.02	16,295
E. Frequency dependent, Preference, best fit ^d	.77	.72	.68	.65	.62	.59	.55	.51	.44	44

^a Difference between observed numbers taken and that expected value, sum of chi-squares for all 9 ratios of prey.

^b Calculated using equation 26 of Murdoch and Oaten (1975): $P = cF/(1 - F + cF)$; where P=proportion expected, c=preference ratio (no. white taken/no. gray taken) at ratio of availability of 5:5 ($124/76 = 1.63$), F=frequency (proportion) of availability of white mice.

^c Calculated using equation of 27 of Murdoch and Oaten (1975): $P = cF_2/(1 - F)_2 + cF_2$.

^d $P = cF_{0.33}/(1 - F)_{0.33} + cF_{0.33}$, exponent determined empirically.

types had only a slight effect on selection. This hypothesis is supported by the facts that expected proportions for a constant, frequency independent preference (Table 7, B) fall outside of 2 standard errors of the mean for observed values only for white:gray ratios of 9:1, 8:2 and 1:9, and that the chi-square value is only a fraction of that for the other 3 ecological hypotheses.

Although it seems unlikely that a predator would prefer to take constant proportions of prey types over a wide range of frequencies this possibility cannot be dismissed, nor can it be distinguished from the following hypothesis with this kind of data and analysis.

An alternative explanation is that preference is reduced at high frequencies and increased at low frequencies by selection or uncommonness. Selection of odd prey is added to overall preference at low frequencies of preferred prey and selection of odd, non-preferred prey is subtracted from preference at high frequencies of preferred prey. If we assume that selection is frequency-dependent, we can obtain an appreciation for the effect of oddity by calculating the preference ratio (C) for the observed proportions of prey taken (P) and comparing this C for the various ratios of prey presented. The equation used in Table 7, B can be rewritten: $C = -P(1 - F)/PP - F$. For a ratio of 9 white:1 gray the observed value of P, 0.80, yields a C of 7.67, which is 4.7× as great as the C of 1.63 observed at the prey ratio of 5:5 and 17.4× as great as the observed C of 0.44 at the prey ratio of 1 white:9 gray. This great change in preference ratio indicates a "switch" in preference, but one which is opposite in direction to that predicted by the switching hypothesis of Murdoch (1969) (Table 7, D).

Murdoch's switching hypothesis has enjoyed considerable popularity, as has apostatic selection (Clarke 1962), which is analogous to switching, and it is reasonable to ask whether there is any evidence for the selection of odd prey other than that provided by my experiments. Salt (1967) in his review of earlier studies suggested that a preference for oddity is the one generalization that encompasses a great variety of experimental results and can be consulted for a review of earlier studies. Murdoch and Oaten (1975) reviewed the results of 8 experimental studies as tests of the switching hypothesis. The number of studies offering evidence for the various hypotheses are: switching (4); frequency-dependent selection (1); frequency dependence in some experiments, switching in others (1); oddity (1); and in various experiments, switching, frequency dependence and oddity (1). Murdoch and Oaten do not recognize the results of Murdoch (1969) and Reed (1969) as representing selection for oddity; they simply note that selection was greater than predicted by frequency dependence at low frequencies and less at high frequencies, and that "...there may be some biological significance in this, although the mechanism has not been studied in these cases." The deviations from expected are small in these experiments, although Reed's (1969) results are statistically significant at the highest density. The fact that evidence for the selection for oddity was found in 25% of the studies examined to show the role of switching should be an adequate testimonial that such evidence does exist, although it is largely unrecognized.

The validity of the results of my first 3 experiments as a generalization about prey selection in raptors is questionable. Experiment 1 can be dismissed because of the poor experimental design and because the data were obtained from only 1 bird. The differences in results and conclusions of Experiments 2 and 3 probably lie in the differences in experimental design. The constantly and randomly changing combinations of substrate color and frequencies of colors of mice in Experiment 2 apparently enhanced selection for conspicuousness and reduced selection for oddity. The infrequent changes of substrate color and the slow and regular changes of proportions of white and gray mice apparently largely eliminated the effects of conspicuousness and enhanced selection for oddity. The most condemning criticisms of my Experiments 2 and 3 are: (a) the experimental de-

signs failed to produce the anticipated results, and (b) the results fail to delineate clearly the relative importance of the SSI and oddity. Since relatively few species of raptors, especially kestrels, regularly select their prey out of a flock or other group of conspecifics, my first 3 experiments thus may have only limited relevance to prey selection by kestrels in the field.

My fourth experiment (Mueller 1975) was designed to determine the relative roles of the SSI and oddity in raptors which encounter their prey one at a time. I presented 1 mouse of a given color 10 times and on the eleventh trial, the kestrel was offered a choice between 1 white and 1 gray mouse. In Part A of the experiment, the first 10 mice were white. This routine was repeated daily, continuing for 15 days after the first gray (odd) mouse was taken or ending at 16 days if no gray mouse was taken. A kestrel could thus select 16 white mice and no gray mice, or 0 to 15 white mice and 1 to 16 gray mice. Part B was a replicate of Part A, except that the first 10 mice were gray and the odd mouse was white.

This experiment tests: (1) whether or not a kestrel has an SSI for gray or white mice, (2) how long an SSI will be maintained when the kestrel is continually faced with a choice between the SSI and oddity, (3) how strong a selection for oddity will be shown once the first odd mouse is chosen. A kestrel with an SSI sufficiently strong to overcome any tendency to select odd mice would choose mice of the same color in both Part A and B while one showing a preference for odd mice would select gray mice in Part A and white mice in Part B. Both parts A and B were performed on a gray substrate and the experiment thus does not test for the effects of conspicuousness, which had essentially no influence on selection in Experiment 3.

Five of the 6 kestrels tested showed clear selection for oddity, and one (Walda) showed obvious selection for the SSI (Table 8). The selectivity index (Manly et al. 1972) for the 5 kestrels selecting odd prey is 11.3 ± 1.09 for Parts A and B combined. The selectivity index would be 1, if there were no (or random) selection, and the \pm indicates the 95% confidence interval.

These statistically significant results indicate that most kestrels have a strong tendency to select odd prey in the laboratory. In addition to the obvious selection for the SSI shown by Walda, the influence of the SSI can be seen in the 5 kestrels that showed selection for oddity. Gandalf and Belle chose only gray mice in Part A. In Part B, they were slow to start taking odd white mice (a mean of 5.5 days) and took an average of 1.5 gray mice in the last 16 trials (Table 8). Thorin, Varda and Bree showed a preference for white mice, choosing white mice in Part A for a mean of 5.7 days and taking an average of 3.3 white mice in the last 16 days. In Part B, these 3 kestrels began choosing odd white mice after a mean of only 0.3 days and took only white mice for the remainder of the experiment.

Experiment 4 thus shows oddity to be considerably more important than the SSI as a determinant of prey selection.

Since the kestrels were not fed until after the last capture of the day, the preference for odd mice could be the result of reinforcement, positive, negative, or a combination of the two. Mueller (1975) presented data and analyses which strongly suggest that reinforcement did not influence selection in these experiments. Can data obtained from kestrels that were forced to capture 11 mice in 1 day be used to comment on prey selection in the wild? Nunn et al. (1976) have shown that wild kestrels, in nature, will capture more mice in a briefer time interval than in my experiments. Several colleagues have questioned my segregation of Walda from the other 5 kestrels in my analysis for selection of oddity. Walda can be added to the sample and the selection index for oddity remains statistically significant: 4.82 ± 2.84 . A few workers have questioned the validity

Table 8: Experiment 4: prey selection in captive kestrels.

Kestrel	Part A: Ten white mice, then choice		Part B: Ten gray mice, then choice	
	No. white chosen before first gray	No. gray taken last 16 experiments	No. gray chosen before first white	No. white taken last 16 experiments
Gandalf	0	16	2	15
Belle	0	16	9	16
Thorin	7	13	0	16
Varda	7	12	1	16
Bree	3	13	0	16
Walda	16	0	0	12

of my experimental design in which a variable number of choice trials (up to 16) are run and results are used to test for the selection for oddity only after the first odd mouse was taken. I have consulted with several statisticians, both before and after the experiments, and all have agreed that the design is valid for the hypotheses it examines. As for oddity, the experiment comments only on selection after the first odd mouse is taken. A better criticism of the experiment is that it took the 5 kestrels (omitting Walda) a mean of 5.6 days to select mice of their non-preferred color. During these 5.6 days they saw a mean of 5.6 odd mice and captured a mean of 61.6 mice of the preferred color (56 were taken when the bird had no choice). If kestrels in nature require more than 5 choices between odd and common prey before they begin taking odd prey, then odd prey will not be taken until it becomes somewhat common. This criticism can be addressed best by considering another: my experiment involved a simultaneous choice between 2 types of prey. In nature, kestrels probably see prey usually one at a time and decide whether or not to attack. If this is true, one can seriously question the relevance of my experiments. On the other hand, if kestrels tend to perceive only one type of prey in the laboratory (as I suggested in my discussion of the SSI earlier in this paper), then one can argue that odd prey are less likely to be perceived in the laboratory than in nature, because of the very limited movement of prey in my experiments. Thus, odd prey may be more likely to be taken in nature than was shown in my laboratory experiments. If this is not true, then oddity may be of relatively little importance in prey selection.

Ideally, prey should be presented to kestrels one at a time and some measure of the tendency to attack be used as the indicator of selection. The only reasonably quantitative measure of tendency to attack is the latency, with a short time suggesting a rapid choice or desirable prey and a long time suggesting a difficult decision or undesirable prey. I measured latencies in all of my experiments, but the statistics I used for analysis produced confusing and inconsistent results. The variance in latencies within and be-

Table 9: Experiment 4: in kestrel prey selection. Time differences in choices: latency for trial 11 (choice trial) subtracted from latency for trial 10 (last no choice trial).

Kestrel	Common mouse chosen	Odd mouse chosen
	Mean \pm standard deviation ^a	Mean \pm standard deviation ^a
Gandalf	-0.0409 \pm 0.7720	0.0265 \pm 0.0404 ^{bc}
Belle	0.0702 \pm 0.1486	0.0553 \pm 0.1042 ^b
Thorin	-0.0330 \pm 0.0664	0.0934 \pm 0.2567
Varda	-0.0478 \pm 0.1626	0.0333 \pm 0.0633 ^{bc}
Bree	0.0334 \pm 0.0995	0.0734 \pm 0.1044 ^b
Walda	-0.0708 \pm 0.1942	-0.0539 \pm 0.1604
TOTAL	-0.0269 \pm 0.1606	0.0478 \pm 0.1398 ^{bc}

^a Times are in decimal hours.

^b Difference between trials 10 and 11 significant, matched-pairs t test, $p < 0.05$, two-tailed.

^c Significant difference between differences for common and odd mice, t test, $p < 0.05$, two-tailed.

tween birds was great and few conclusions could be drawn concerning the experimental variables. For this review, I have re-analyzed the latencies for Experiment 4 in several different ways and present the results of the most informative method in Table 9. The datum used is the difference in latencies between the choice trial (11) and the immediately preceding no-choice trial (10). Latencies tend to be similar in adjacent trials, and this method reduces the extraneous variance.

Overall, the results of this analysis confirm the results based on the type of mouse selected. For all 6 kestrels pooled, latencies were slightly longer when common mice were chosen, and significantly shorter when odd mice were chosen, than in the previous no-choice trial. The difference between these differences is statistically significant ($p < 0.001$). However, the latencies provide less consistent results than those obtained from the type of prey taken. Only Gandalf and Varda show individually significant differences in latency differences (Table 9) whereas all but Walda selected significantly more odd than common mice (Table 8). Inconsistent with each other and the fact that only Walda failed to show selection for odd mice are the following: (1) both Thorin and Walda failed to show a significant difference in latencies between trials 10 and 11 when odd mice were taken, (2) only Belle failed to show a relatively shorter latency for choices of odd mice than for choices of common mice, and (3) only Belle and Bree took longer to capture mice on trial 10 than on trial 11 when common mice were chosen. In spite of these inconsistencies, I am now reasonably optimistic that a carefully designed experiment presenting prey one at a time may produce results showing prey preferences in kestrels. Such an experiment might also alleviate a real problem with my experiments: extremely long latencies in many trials. The totals in Table 9 show a mean latency of 1'36" longer for trial 10 than trial 11 when common mice were taken, and similarly, 2'05" shorter when odd mice were taken. Note that these are differences and not actual times.

The long latencies in my experiments primarily were caused by the kestrels' dislike of capturing mice from the pedestals (the occasional mouse that jumped or fell from a pedestal was usually pursued immediately). It should be possible to eliminate the necessity for pedestals by monitoring carefully the activity and position of a single mouse. An experimental design with fewer trials each day might also reduce latency. My fifth and last experiment (Mueller 1977) was an attempt to determine whether odd species would be selected more often than abundant ones. I used albino laboratory mice and 1 to 3 day-old domestic chicks as prey. The experimental design was identical to that of Experiment 4, except that the chicks were substituted for the gray mice.

Four kestrels showed a clear selection for oddity (Table 10), with a selection index (Manly et al. 1972) of 7.53 ± 2.33 for Parts A and B combined. Three kestrels showed a definite selection for an SSI for chicks (Table 11), with a selection index of 23.0 ± 1.05 for Parts A and B combined.

The selection shown by the 2 groups of kestrels is completely different and justifies their segregation and separate consideration. The preference of Gildor, Walda and Gandalf for chicks is not due to a preference for the taste of chicks. In a separate experiment, I offered the 7 kestrels a dead mouse and a dead chick twice daily for 20 days. The kestrels fed on chicks on only 12% of the feedings (including cases when they fed on both chicks and mice), and chicks constituted 7% of the total weight of food consumed. There were no significant differences between individuals in the incidence or amount of chick consumption. The only likely explanation for the preference for chicks shown by the 3 kestrels is that chicks are easier prey. Mice struggle more vigorously than chicks when captured and can inflict painful and damaging bites. The results thus show a selection for oddity in 4 kestrels and a preference for easy prey in 3. Perhaps kestrels will select the odd species, but that other factors may overwhelm the preference for oddity. This experiment is subject to all of the criticisms that I discussed for Experiment 4, with the added caveat that all selection disappears if one pools the results of the kestrels that selected odd prey with those that selected easy prey.

OTHER LABORATORY EXPERIMENTS

Ruggiero and Cheyney (1979) and Ruggiero et al. (1979) reported the results of a complex experiment designed to detect the interaction of various prey characteristics in selection of prey by kestrels. The characteristics tested were color, movement and morphology. Each of their mice was: (1) black or white, (2) dead (and hence no movement), drugged (abnormal movement), or normal, and (3) of normal morphology or with a 1.2 cm cotton ball affixed to its back and a 7.5 cm piece of yarn tied to its tail, both of the same color as the mouse. Two colors \times 3 types of movement \times 2 morphologies yield 12 different kinds of mice. Only 66 choice trials were performed in the experiment and each kind of mouse thus appeared only 11 times and only once paired with another particular kind of mouse. This small sample is inadequate to evaluate the individual influences of all 7 variables that were tested.

From the above, Ruggiero et al. (1979) concluded that their experiments indicate the following: (1) raptors do not generally select prey only on this basis of conspicuousness, (2) there is a significant interaction between prey characteristics, (3) analysis for potential interactions is very important, (4) predator experience (pre- and experimental) is critical in assessing the influence of prey characteristics, (5) prey items that are not discontinuous with a kestrel's experience are selected significantly more often, (6) oddity, if it means novelty, reduces the probability of attack, (7) movement decreases selection for unfamiliar morphs, (8) aberrant movement is more an attack stimulus than normal movement, (9) prey movement is a most important factor.

Table 10: Experiment 5: selection for oddity in prey taken by captive kestrels.

Kestrel	Part A:		Part B:	
	No. mice chosen before first chick	No. chicks taken last 16 choices	No. chicks chosen before first mouse	No. mice taken last 16 choices
Bree	0	6	6	15
Pippin	0	13	0	14
Varda	1	12	1	16
Belle	9	11	1	16
Mean	2.5	13.0	2.0	15.3

Table 11: Experiment 5: selection for SSI in captive kestrels.

Kestrel	Part A:		Part B:	
	No. mice chosen before first chick	No. chicks taken last 16 choices	No. chicks chosen before first mouse	No. mice taken last 16 choices
Gildor	0	16	2	14
Walda	1	16	16	16
Gandalf	2	16	7	14
Mean	1.0	16.0	8.3	14.7

I have no argument with the first conclusion except to note that their experiments were not designed to test conspicuousness: the dark brown peat-moss used as a substrate did not match the color of either the black or white mice. The second and third conclusions are supported by their finding of a statistically significant interaction between movement and morphology ($x^2 = 15.04, p = 0.01$, but see below). I agree in principle with the fourth conclusion, but Ruggiero et al. (1979) failed to show that their experimental design resolves the problems of the effects of pre- and experimental experience. They began testing their kestrels 2 days after they were captured and used each of 4 birds in 16 or 17 trials in an undescribed sequence of choices.

I question conclusions 5 and 6 as valid generalizations, although they are supported by their data. These conclusions are based on: (a) the preference for the familiar over

the unfamiliar morph and (b) the preference for black mice over white mice (black mice resemble wild mice more than albinos). The preference for the familiar morph is shown only in live mice: 28 of 44 familiar morphs, and only 7 of 44 unfamiliar morphs were taken ($\chi^2 = 18.98, p < 0.0001$). No difference was shown in dead mice: 10 of 22 familiar morphs and 15 of 22 unfamiliar morphs were taken ($\chi^2 = 1.48, p > 0.20$). The unfamiliar morph used by Ruggiero et al. (1979) is an artifact which does not resemble any naturally occurring prey of kestrels. Kestrels indubitably learn characteristics of prey; they had no chance to learn the characteristics of this unfamiliar morph prior to the experiment and only limited opportunity within the experiments. Moreover, Mueller (1974b) has shown that at least the basic features of prey recognition are innate. Naive, hand-reared kestrels did not prey upon simple models, including mouse-like models, but did prey upon live mice. Ruggiero and Cheyney (1979) noted that kestrels actually retreated from their unfamiliar morph, suggesting that unfamiliar morphs are an aversive stimulus. Thus their results do not provide evidence on the influence of novelty on prey selection within the limits of naturally occurring variability of prey.

The preference for black, rather than white mice shown in their experiment can be attributed to a preference for familiar mice if we accept the contention that black mice are more similar in appearance to wild mice than white mice. However, the black mice were of a different genetic strain than the white mice and may have possessed some behavioral characteristic that rendered them more attractive to kestrels than white mice. The various genetic strains of laboratory mice exhibit many differences in behavior (Sprott and Staats 1975). This is a distinct possibility in the experiment of Ruggiero et al. (1979): their kestrels took 18 of 22 live, black mice of the normal morph and only 10 of 22 live, white mice of the normal morph ($\chi^2 = 4.81, p < 0.04$). There was no color preference shown with dead mice: 15 of 22 black mice and 10 of 22 white mice were taken ($\chi^2 = 1.48, p > 0.20$). Thus, black mice were preferred only when alive. Their kestrels may have preferred black mice because they were more familiar and this was obscured in dead mice because white mice were more conspicuous than black mice. This explanation requires that conspicuousness is significantly more important in dead than in live mice.

Conclusion 7 is supported by their results, but the explanation for the interaction of movement and morphology is not supported by the data. Ruggiero et al. (1979) proposed that: "An unfamiliar prey item has high arousal potential. Theoretically, this arousal level is increased by movement and the upper arousal level is exceeded." If unfamiliar non-moving prey has high arousal potential, then the kestrels should take more dead, unfamiliar morphs than dead, familiar morphs. This was not the case. A much simpler, and more likely explanation is that the cotton ball and piece of yarn were not perceived as a part of the dead mouse by the kestrels, but instead appeared to be objects in the environ of the mouse. Perhaps the 7 of 44 moving, unfamiliar morphs taken by their kestrels were not moving when the selection was made; Ruggiero et al. (1979) did not provide information to assess this possibility. Also, the kestrels may have learned to recognize the unfamiliar morph by first preying upon dead, unfamiliar morphs.

Conclusion 8 is not supported by the data. The 20 drugged, abnormally moving mice taken do not differ significantly from the 15 normally moving mice taken. If we restrict consideration to the familiar morph, 16 abnormally moving mice and 12 normally moving mice were taken by the kestrels, and this also is not a statistically significant difference. I have conducted a number of pilot experiments with mice injected with various drugs and found no suggestive evidence that that kestrels might select abnormally moving mice when the frequency and amount of movement were measured and considered as

variables influencing prey preference. I believe that abnormal movement does influence prey selection, but I have been unable to find an experimental design using mice and kestrels which provides unequivocal results.

The ninth conclusion is the only one which they qualify as "a most important factor", yet there is no evidence that movement was monitored carefully in their experiments. The experiments were conducted in 6x3x3 m aviaries with solid, gridded sides and peat moss substrates. The grid size was unspecified. Movement was measured by the number of grid lines crossed. No indication is given of the position of the observer. My experience in attempting to monitor the behavior of mice in selection experiments involving drugged mice has convinced me that filming, or videotaping, and frame by frame analysis are probably necessary for an adequate appraisal of the effects of movement on prey selection.

There is one other laboratory study of kestrels relevant to the problem of prey selection. Sparrowe (1972) trained kestrels to attack a moving, mouselike model. He varied the distance (and hence the time) the model was exposed to the kestrel, the contrast of the model relative to the substrate, and the amount of "cover" (strips of paper over the path of the model). Sparrowe used 12 wild-trapped kestrels, 4 each to test the influence of each of the 3 factors. In his initial trials with the birds, all 3 factors influenced the number of predatory attempts significantly ($p < 0.05$), but not success in capture. He then performed a series of learning-rate tests in which he decreased exposure time and contrast, and increased cover, each stepwise, until maximum performance was attained by each bird. These experiments yielded significant results only for exposure time, where both predatory attempts and success in capture declined significantly ($p < 0.05$). Sparrowe next tested 10 of his kestrels in an experiment combining the effects of cover and prey contrast. A comparison of no cover and 60% cover, and 4 levels of reflectance of prey showed a highly significant effect of prey contrast with substrate ($p < 0.001$). Thus, prey contrast and cover were of importance only when combined. The only significant main effect was prey exposure time. Sparrowe concluded that kestrels can adapt to rapid changes in prey contrast and cover density, but not to rapid reductions in prey exposure time. The situation may be similar in the field. We lack data for kestrels, but Kaufman (1973) has shown that cover, conspicuousness, and distance influence the color of mice selected by Loggerhead Shrikes (*Lanius ludovicianus*). Kaufman released one agouti and one albino mouse within the view of a perched shrike in the field. At near distances and in sparse vegetation, there was a significant preference for agouti mice ($p < 0.01$). At a greater distance, or in dense vegetation, white mice were preferred ($p < 0.05$). Distance can have much the same effect as cover, both reducing the noticeability of prey.

Sparrowe (1972) also tested 3 hand-reared kestrels. The entire predatory experience of his hand-reared kestrels was with his experimental models, and these birds showed no consistent differences in attempts to capture the model with varying experimental treatment; only the rate of success changed with increased difficulty of capture. The predatory attempts of wild-caught birds decreased with increasing difficulty of prey detection and capture as well as some decrease in success per attempt. The hand-reared birds attempted, and often successfully captured, the model under experimental conditions where a wild-caught bird would not make an attempt. The wild-caught birds had presumably learned to avoid trying to capture difficult prey and the hand-reared birds had insufficient experience with difficult and potentially dangerous situations to acquire such a discrimination. Overall, Sparrowe's results suggest that kestrels learn to evaluate their chances of prey capture and are more likely to initiate an attack when it is likely to be successful. These results are akin to my conclusion that some kestrels learn to prefer less dangerous prey when confronted with a choice between chicks and mice (Mueller 1977).

FIELD EXPERIMENTS

I know of only one published account of field experiments on prey selection in kestrels (Bryan 1984). Bryan placed a mouse in each of 2 bal-chatris separated by 15 cm on a common base and dropped the trap 10–40 m from a kestrel. When an agouti mouse was placed in one bal-chatri and a white mouse in the other, 73 kestrels attacked agouti mice and only 16 selected white mice. This is strong evidence for the selection of familiar, or SSI mice ($p < 0.005$), and offers little support for the selection of odd, or novel mice in a more natural situation than exists in the laboratory. However, Bryan noted that the kestrels appeared to be making a deliberate selection and thus 18% appeared to prefer odd mice. The selection shown by Bryan's kestrels does not differ significantly from that by my kestrels on the first day of parts A and B, combined, of Experiment 4 (Table 7): odd mice were taken in 5 cases and common mice were taken in 7 cases ($\chi^2 = 2.31, p > 0.10$). Five of the 6 birds eventually showed a significant preference for odd mice; in the 6 cases where this was not shown initially the switch occurred at a mean of 4.8 days. The ratio of agouti mice to white mice attacked by Bryan's kestrels does not differ significantly ($\chi^2 = 3.11, p > 0.07$) from the ratio of black to white mice of the normal morph (25:13) taken by the kestrels of Ruggiero et al. (1979). The agreement between the results of 3 quite different experiments suggests the possibility that the SSI overwhelms the preference for oddity in most kestrels, at least when the color of mice are what determines the SSI and oddity.

Bryan also performed experiments offering kestrels 2 sizes of agouti mice: small (22–27 g) and large (35–40 g). Whenever possible the weight difference between the mice used was 15 g. The results of these experiments are enigmatic. Bryan found no size preference in either males or females in winter (Sept.–Dec., Table 12). In summer (May–July), adult females attacked significantly more large mice ($\chi^2 = 11.56, p < 0.001$) and adult males selected significantly more small mice than expected if selection were random ($\chi^2 = 11.57, p < 0.001$). Juvenile females attacked significantly more small mice than expected (Binomial test, $P = 0.046$). The sample size is insufficient for juvenile males. The selection of small mice by recently independent young kestrels probably represents an avoidance of larger and potentially more dangerous prey. Bryan suggested 3 hypotheses that might explain the preference of adult males for small mice and the opposite preference of adult females for larger mice: (1) The sexes are avoiding competition with each other; (2) Small mice are more abundant during the summer and males, which do most of the hunting for the family, have formed an SSI for small mice. Females have not formed an SSI and select large mice to maximize energy gain; (3) Males hunt at considerable distances from nests, and it may be more efficient to transport smaller mice. Females hunt infrequently near the nest and transport distances are short. I can think of only one hypothesis to add to the above: the slow and labored flight necessitated by the carrying of large prey may render the male more attractive and vulnerable to piracy by other raptors. I think the first hypothesis is unlikely and I remain unconvinced by any, including mine. Further experiments are needed, perhaps with small enclosures for mice that would permit capture and transport, placed at known distances from active kestrel nests.

Bryan separated the kestrels he captured into "underweight" and "overweight" classes. He computed the ratio of mean wing chord to the cube root of mean body weight for each sex. Any bird below the mean was considered overweight and any above the mean, underweight. In winter, underweight females attacked significantly more large (and fewer smaller prey) than overweight females ($\chi^2 = 5.18, p < 0.025$). Bryan suggested that hunger influenced the selection of size of prey selected by females in winter. Mueller (1973) found a clear relationship between food deprivation time and the ten-

Table 12: Numbers of large and small mice selected by wild kestrels in the field experiments of Bryan (1984).

Kestrels		Large	Small
Males	Sept. - Dec.	23	26
Adult males	May - July	5	23
Juvenile males	May - July	1	1
Females	Sept. - Dec.	41	49
Adult females	May - July	21	4
Juvenile females	May - July	3	10

dency to kill mice by kestrels tethered in the laboratory. His kestrels did not kill mice if they had cached food available. Nunn et al. (1976) tossed out mice from an automobile near a female kestrel in southern Illinois in January, and the bird killed 20 mice in 1.05 h. Most of the mice were cached and the kestrel did not begin to eat until 0.55 h after the last mouse was killed. These results suggest that hunger may have little effect on the predatory behavior of kestrels in the field and the possibility that hunger might influence the size of prey taken should be considered with great caution.

Mueller and Berger (1970) found that migrating male Sharp-shinned Hawks (*A. striatus*) that struck European Starlings (*Sturnus vulgaris*) were lighter in weight than those that struck House Sparrows (*Passer domesticus*). The 7.3% difference was significant for juvenile males ($t = 2.97, p < 0.005; N = 7.97$), but the 4.3% difference was not significant for adult males (Mann-Whitney $U = 56, p > 0.27, N = 2; 103$). The sample size for adult males striking starlings is very small, but it is doubtful that a larger sample would yield significance. Females not only failed to show a significant difference, but the weight of those that struck starlings was actually slightly higher than the weight of those that struck sparrows (juveniles, 0.5%; adults, 0.9%). The mean weight of starlings is 84%, 80%, 50%, and 47%, respectively, of the mean weight of juvenile male, adult male, juvenile female and adult female Sharp-shinned Hawks. The respective percentages for House Sparrows are: 34, 27, 17, and 16. It appears that hunger only influences the size of prey taken when: (1) the prey exceeds 80% of the weight of the hawk, and (2) the hawk is young and relatively inexperienced.

The mean weight of Bryan's large mice was 35% and 31%, respectively, of the mean weights of his male and female kestrels. The respective percentages for small mice are 23 and 20. It is difficult to believe that hunger influenced the choice of size of prey only in females. I suggest an alternative hypothesis: the difference found by Bryan is the result of adult females preferring large mice and juvenile females selecting small mice. No difference was shown by males because most juvenile males were excluded from the areas trapped by Bryan in winter by socially dominant females and adult males. This hypothesis requires further experiments for verification. Sharp-shinned Hawks do show age differences in the size of prey preferred (Mueller and Berger 1970). Mueller and Berger trapped Sharp-shinned Hawks using European Starlings and House Sparrows as lures. An attacking hawk could either strike the lure and be caught in a bownet, or

stoop within less than 2 m of the lure and be caught in a dhogazza (or pass at a greater distance, and not be included in the analysis). I have re-analyzed the data used by Mueller and Berger, revealing some peculiar interactions of age and sex in the size of prey attacked. Of the attacks on sparrows or starlings, 13.1% of 328 adult males, 13.5% of 408 adult females, 11.6% of 319 juvenile males, and 19.3% juvenile females attacked starlings. Significantly more juvenile than adult females attacked ($\chi^2 = 4.41, p < 0.04$), but there was no difference between the ages in the males ($\chi^2 = 0.43, p > 0.50$). Juvenile females attacked starlings more often than juvenile males ($\chi^2 = 7.09, p < 0.01$), but there was no difference between the sexes in the adults ($\chi^2 = 0.01, p > 0.90$). Of the hawks that attacked starlings, 5.6% of the adult males, 23.6% of the adult females, 18.9% of the juvenile males, and 53.4% of the juvenile females actually struck the starlings. Adult females struck a higher proportion of starlings than adult males ($\chi^2 = 4.33, p < 0.05$), but the difference between the sexes was much greater for juveniles ($\chi^2 = 10.64, p < 0.002$). Juvenile females struck a much higher proportion of starlings than adult females ($\chi^2 = 10.34, p < 0.002$), but the difference between the ages in males was not quite significant (Fisher exact probability, $p = 0.058$). Thus, juvenile females attacked more, and struck more large prey than adult females, which agrees with the hypothesis I have suggested for Bryan's results with kestrels. Overall, the age difference in size of prey taken is as great, or greater than any difference between the sexes. Sex differences are great in juveniles, but relatively slight in adults. This is surprising because the Sharp-shinned Hawk is the most dimorphic species of Falconiformes found in North America: the mean weight of adult males is only 59.2% of that of adult females. One would expect sex differences in the size of prey to completely overwhelm age differences in such a dimorphic species. We need more data on the influence of age and sex on prey preference.

EVIDENCE FROM FIELD STUDIES

An important question to ask is whether the various laboratory experiments have any relevance to prey selection in wild, free-living kestrels. Laboratory experiments can only suggest what might be happening in the wild, and these suggestions should be confirmed by field observations. Unfortunately, it is impossible to determine exactly what a kestrel perceives to be available as prey at the time it performs a selection in the complexity existing in a natural situation. Thus, field observations also offer only suggestions about the process of prey selection.

Kestrels do show a tendency to specialize upon a given type of prey for long intervals of time, and this tendency could be interpreted as an SSI. Anyone who has trapped kestrels with a bal-chatri baited with a mouse knows that the birds are easiest to trap in winter when insect prey is non-existent, and most difficult to trap in late summer and early fall when grasshoppers are abundant (Berger and Mueller 1959). At the Cedar Grove Ornithological Station in Wisconsin we use a variety of birds as lures to capture migrating raptors, including House Sparrows, European Starlings, and occasionally Common Grackles (*Quiscalus quiscula*).

Migrating kestrels are much easier to capture in spring than in autumn. In 1953-56, we observed 286 kestrels in autumn and caught 17, or 5.94%. In spring, we observed 670 and caught 79, or 11.79%. Our blind and traps are permanent structures and the entire operation is designed for the trapping of southbound raptors. Northbound birds are rarely seen before they are over or slightly beyond our traps and are thus difficult to lure and capture. Only 125 of the 670 kestrels observed in spring were southbound birds. In autumn, essentially all kestrels are southbound, and the most appropriate comparison is with southbound birds in the spring: thus, kestrels are 5.25 times more likely to be

caught in spring than in autumn.

Insects are extremely scarce at Cedar Grove through the entire period of the spring migration of kestrels and most of the birds have also just experienced a winter with little or no insect prey available. In contrast, grasshoppers and other insects are abundant in Wisconsin through most of the autumn migration of kestrels. Although most kestrels pass over our traps in autumn without showing any interest, we frequently have attracted a kestrel with our lures only to have it hunt grasshoppers in our trapping area and then depart southward, uncaptured. Trapping kestrels in autumn at Cedar Grove usually involves the bird aborting its initial attack and perching for a prolonged period, frequently aborting several more attacks before being captured. The situation is dramatically different in the spring when most kestrels approach the lures directly and rapidly, often from distances well over 100 m and usually bind to the lure on the first attack. We have captured more than a few kestrels on European Starlings in spring and a few on Common Grackles. Attacks on lures this large are extremely rare in autumn. In short, kestrels attack birds much more often in the spring than in the fall and often with a dash and verve resembling that of the Merlin (*F. columbarius*).

Page and Whitacre (1975) observed 3 kestrels that were specializing largely on shorebirds, mostly Least Sandpipers (*Calidris minutilla*) for a period of 7 weeks in mid-winter. Freer (1973) found that about 35 Bank Swallows (*Riparia riparia*) were taken from a nesting colony by a kestrel (or kestrels) in 5 days. Likely, only 1 pair of breeding kestrels was involved in the predation on this swallow colony and thus the pair and its young were probably subsisting exclusively on Bank Swallows during the 5 day period. Windsor and Emlen (1975) presented observations which suggest that the findings of Freer are not unique.

Balgooyen (1976) noted a shift in the prey preferences of kestrels through the spring and summer in the Sierra Nevada: birds and mammals were taken early in the season, then lizards and insects, and finally, largely insects. Balgooyen stated that the kestrel's switch to insects is rapid and coincides with the first appearance of winged grasshoppers. The documentation for this statement is in his Fig. 22, which presents data lumped for 11-day intervals. Eleven days is too long an interval to evaluate the possibility that the transition from vertebrate prey to insects lagged slightly behind the sudden appearance of grasshoppers, which would provide better evidence for the existence of an SSI (Tinbergen 1960). Collopy (1973) found that kestrels in Humboldt Co., California, showed significant switches in prey from invertebrates in October and November to vertebrates during an unusually cold December and back to invertebrates in January and February.

Kestrels apparently prefer to specialize on reasonably large insects, particularly grasshoppers, that can occur commonly in the open habitats preferred by the birds. When insects are unavailable, kestrels are able to specialize on small mammals or even birds with an efficiency which is at least sufficient for survival. In 1947, I watched a pair of kestrels that nested in a cavity in a roof ornament on a 9-story building in downtown Milwaukee, Wisconsin. This pair appeared to be preying largely on House Sparrows (several were observed to be caught in flight). The kestrels successfully fledged 3 young. Apparently, kestrels can catch birds with sufficient efficiency to rear a brood if few other prey are available.

The data from the various field studies cited above indicate that kestrels often show a tendency to specialize largely on a given type of prey for extended periods. Although this evidence fails to provide a robust proof of the SSI hypothesis, it is certainly consonant with the concept.

There also is evidence from the field to support the hypothesis that kestrels select

odd prey. One of 271 prey items recorded in Heintzelman's (1964) study of kestrel food habits was a Skink (*Eumeces fasciatus*), a species not known to be present in the area. Records of extralimital or rare small mammals are frequently reported from raptor pellets or remains in nests (see, e.g., Schwartz and Schwartz 1959).

In Freer's (1973) study, all of the approximately 35 Bank Swallows taken by the kestrel(s) appeared to be young birds. Recently fledged swallows are less adept fliers than adults, and Freer's observations suggest that the kestrel(s) recognized this "odd" behavior and selected young birds and did not attempt to capture the much more numerous flying adults. Both Freer (1973) and Windsor and Emlen (1975) observed kestrels attacking swallows in mist nets, and the behavior of a swallow in a mist net is certainly odd.

Anderson (1968) observed a kestrel capture a wounded Brown-headed Cowbird (*Molothrus ater*). The kestrel had not made any predatory attempts on the individuals in a mixed flock of cowbirds and Red-winged Blackbirds (*Agelaius phoeniceus*) before the cowbird was shot. Harris (1965) saw a Eurasian Kestrel (*F. tinnunculus*) capture a starling that was blind in one eye out of a flock of conspecifics.

Bats have a fluttering and erratic flight which is odd in comparison to that of birds. Bats rarely fly in daylight, but when they do, they are extremely attractive prey for kestrels and other diurnal raptors (Mueller 1968b). I have released bats in daylight in homing experiments and observed kestrels capturing bats on 4 occasions; in one case a male kestrel captured 3 bats in less than 20 minutes. D.D. Berger and I have designed and developed traps for migrating hawks at the Cedar Grove Ornithological Station. We believe that our manipulation of lure-birds, resulting in odd wing-flapping behavior, is a key part of our high success rate in attracting and capturing kestrels and other raptors.

In all of the field observations listed above, odd prey are also easy prey. The problem with observations such as that of Harris (1965) is that the half-blind starling may simply have been easier to capture than fully-sighted individuals and that no selection was involved. Mueller (1974a) lists a number of similarly equivocal observations for other species of raptors.

The available evidence from both the laboratory and the field thus suggests that kestrels show 2 opposing tendencies in prey preference: a tendency to specialize on a given type of prey, which may be due to an SSI, and a tendency to select odd prey. Specialization probably permits more effective foraging in a variety of ways. Search time is probably reduced because it is easier to find prey if the identity, habits and habitat of the prey are known. A SSI probably permits rapid recognition of prey amid the visual clutter of the natural environment. Proficiency in capture and killing of prey are likely enhanced. Lastly, selecting prey which can be captured at low risk of injury to the predator and which is sufficient for metabolic needs is obviously better than taking chances by preying randomly.

The SSI concept virtually has been ignored in recent foraging theories and models, largely because Tinbergen's (1960) imperfect mathematical formulation of his SSI model has failed to explain ecological data on predator-prey population interactions (Royama 1970, Murdoch and Oaten 1975), and because the verbal description of his hypothesis and its ecological implications have been found to be too vague to be useful (Landenberger 1968, Dawkins 1971). Murdoch and Oaten (1975) noted that Tinbergen appeared to be simultaneously demonstrating a behavioral phenomenon and evaluating its population consequences, and that the behavioral component may still be useful even though the ecological portion of the hypothesis has proven to be inadequate. Switching theory (Murdoch 1969, Murdoch and Oaten 1975) has replaced the SSI as an explanation for relatively sudden shifts in prey preference where the ratio of prey types taken differs

from the ratio of prey abundance. Cornell (1976) noted that switching involves "factors analogous to those which induce the formation of a search image" and proposed that switching "is an optimization of two processes: search image formation and flexibility in prey species selection." This idea of a flexible searching image is consonant with the available information on prey selection in kestrels. Learning has been included in models of optimal foraging (Hughes 1979), and the formation of a SSI can be regarded as learning to see prey (Dawkins 1971). The behavioral concept of the SSI is thus not in conflict with optimal foraging theory. Additional evidence for the SSI can be found in Croze (1970) and Mueller (1974a).

The selection of odd prey also may be an optimal strategy. At the level of optimal foraging theory, odd prey is profitable because it usually is easier to capture. At a more arcane level, preying upon odd prey may tend to drive predator-prey systems towards the maximization of yield. In nature, odd prey is almost invariably unfit (e.g., ill, injured, in the wrong habitat, etc...). Unfit animals are unlikely to contribute to the growth of the prey population and a "prudent predator" should select those individuals with low reproductive potential (Slobodkin 1968). Burckhardt (1953), Errington (1963, 1967), Blondel (1967) and others have suggested that predators act as "managers" of their prey for the benefit of the prey population as well as for the predator. Many questions remained to be answered about prey selection in kestrels and other raptors. Every detail should be recorded in casual field observations and further studies in the field should be designed to gather data pertinent to the various hypotheses. Further experiments should recognize the limitations of the laboratory as a comment on nature and yet make every effort to exploit the controlled conditions possible.

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A STUDY AND IMPLICATIONS OF HABITAT SEPARATION BY SEX OF WINTERING AMERICAN KESTRELS (*Falco sparverius* L.)

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Abstract: Counts of wintering American Kestrels in central California indicate that males occupy areas with relatively higher vegetative cover than females. This habitat separation may not relate to hunting patterns, hunting success, or selection of prey. Dissimilarities between male and female territories include a higher density of birds and mammals/hectare on females' territories. Based on our findings, an evolutionary strategy is proposed that hypothesizes how a monomorphic species developed into a sexually size and color dimorphic species. Winter habitat separation by sex is a result, not a cause, of sexual size dimorphism in kestrels. We suggest that a "habitat split" occurs intersexually, as distinguished from a "niche split".

Observations of wintering kestrels show habitat separation by sex. Balgooyen (1972, 1976) noted many female kestrels in open areas of the Hollister Basin, San Benito and Santa Clara Counties, California. In northern California, Koplin (1973) observed male kestrels residing in wooded habitats and females in open habitats. Mills (1976) detected a similar division by sex in open and wooded areas of Texas and Arizona as did Stinson et al. (1981) in Georgia's wintering kestrels.

While Koplin (1973) proposed that competition for food would be reduced between the sexes, Mills (1976) felt that female domination of the male allowed her to secure the "better" habitat. In order to evaluate these hypotheses, we studied the activities of 5 male and 5 female kestrels in winter territories. This study reports hunting techniques, food items, prey densities, predation successes, territory sizes, and territorial vegetational preferences of male and female kestrels and suggests reasons for differential habitat utilization by sex.

STUDY AREA AND METHODS

The Hollister Basin of northern California lies in Santa Clara and San Benito Counties. The 150 km² study area ranged in elevation from 48 m to 210 m.

During late fall and winters of 1976-1977 and 1977-1978, 10 individuals were trapped within their territories in late fall (see Berger and Mueller 1959) and banded with U.S. Fish and Wildlife Service bands. Marked leather flags, secured to tarsi, aided in identifying individuals in the field. Observations ran from dawn to dusk; occasional half-day sessions were recorded. Field observations were logged and later transcribed into a permanent field notebook. Total observation time was nearly five hundred hours.

The mark-recapture method (Smith 1974) provided an estimate of the density of small mammals. During winter, 50 Sherman live-traps placed at 4.6 m intervals were set along a line transect in each kestrel's territory. During the 1976-1977 winter, trapping was performed from 17 December through 20 February; during the 1977-1978 winter, traps were set 18 November through 5 February. A total distance of 2125.4 m was sampled during each transect, and each kestrel territory was sampled at 2-week intervals. Traps set between 1500 and 1700 were checked late that night and the following morning. Captured mammals were individually marked by the removal of a toe (see Martof 1953).

Traps were then set in the same location during the second afternoon. The calculation for the total density of small mammals follows:

$$\text{population estimate} = \frac{\text{total animals day 2} \times \text{animals day 1}}{\text{marked animals day 2}}$$

A line transect measuring 1.9 by 2104.5 m (1 acre) was sampled from November through February to estimate numbers and kinds of prey in each territory. At weekly intervals, insects were collected from each transect with a beating net, then identified, weighed, and counted. During sampling of insects, the number of birds within or flying across the line transect was recorded.

A mean prey weight was applied to invertebrates in order to obtain the total weight of prey eaten. Where indicated, a 0.2 g weight was used for unknown invertebrates; this represents the mean insect weight taken by kestrels. The mean weight was calculated from available insects from transects and weighted according to the relative numbers and kinds of insects found in kestrel pellets. A 3.5 g mean weight was used for Jerusalem Crickets (*Stenopelmatus longispinus*).

The weight of the vertebrate items recorded was the amount of vertebrate prey eaten during the day of observation. Kestrels frequently cached vertebrates; therefore, the total weight of vertebrate prey was not always used. The quantity of the prey items consumed was determined through observation, using a 40 x spotting scope, or by location of the cached prey and estimation of the amount eaten. By using only the weight of prey consumed, a more accurate determination of the proportions of prey categories taken by the sexes could be made. Mean weight of vertebrates was calculated from: 1) mammal census data, 2) bird banding data (L.R. Mewaldt, pers. comm.), and 3) lizard weights reported by Munsey (1972).

Kestrels hunted in different areas of a territory: plowed fields, grazed pastures, alfalfa fields, shoulders of roads, barley fields, fallow areas, vineyards, harvested fields, and apricot and walnut orchards. Estimates of mean plant height and density of cover for each area indicated quantity and quality of cover. For each plot, 3 transects of 91.4 m were sampled randomly along compass headings. Any vegetation over 2.5 cm was arbitrarily considered prey cover. Observations of movements by individual birds defined the boundaries of a territory. The perimeter of each kestrel's territory was walked with a surveyor's measuring wheel to determine the dimensions and total area.

The following activities of kestrels were recorded to determine allotment time by sex:

Active perching: looking for prey from a perch with tightly held feathers and frequently with a "cocked" orientation of the head.

Inactive perching: an upright posturing and/or standing on one foot with feathers held loosely.

Hovering: remaining in a fixed position on flapping wings.

Flying: soaring, flying between hoverings, striking from perches, flushing, and heading for a roost.

Eating: preparing and consuming prey. Prey preparation involves discarding insect appendages, bird feathers, mammal fur, and viscera.

Caching: storing and retrieving prey items. Storage time incorporates leaving a perch with prey, placing of prey item, and returning to perch. Retrieval time includes flying to and searching for a cache, and returning to a perch for eating.

Fighting: responding to either offensive or defensive actions.

Hunting from a perch: searching from a perch and striking at a prey on the ground.

Hawking from a perch: flying from a perch striking airborne prey with the feet and returning to the same perch.

Table 1: Hunting techniques of male and female American Kestrels in California.

Kestrel sex	Hunting method	Number of strikes				Success Ratio(%)	% of Total
		Total	Successful	Unsuccessful	Unknown		
Female	Perching	1700	494	828	378	37.4	84.1
	Hovering	205	25	52	128	32.5	10.1
	Hawking	19	6	7	6	46.2	1.0
	Soaring ^a	1	1	0	0	100.0	0.0
	Flush-flying	96	5	83	8	5.7	4.8
	Total	2021	531	970	520	35.4	
Male	Perching	1595	484	621	490	43.8	92.7
	Hovering	57	16	21	20	43.2	3.3
	Hawking	17	10	5	1	62.5	1.0
	Soaring ^a	32	24	1	7	96.0	1.9
	Flush-flying	19	4	12	3	25.0	1.1
	Total	1720	538	660	521	45.5	

^a Data on soaring were not statistically included due to the infrequent use of this hunting method.

Hunting from a soar: flapping wings and gliding on rising air currents at a height of 70-600 m. Insect prey is secured with feet and consumed in the air.

Flush-flying: flying rapidly in a low position (0.7-1.5 m) over vegetation for a distance of 30-310 m in an effort to flush small birds.

RESULTS AND DISCUSSION

Hunting by Kestrels. – The Chi-square test indicated a significant ($p < 0.005$) difference between the frequency of hunting methods employed by male and female (Table 1). Both sexes hawked with equal frequency ($p > 0.10$), but females hunted from a hover and did flush-flying with greater frequency than males ($p < 0.005$). More numerous hovering and flush-flying by females may relate to the lack of perch sites over a more open territory. Male kestrels employed perch hunting more frequently than did the female ($p < 0.005$), perhaps due to the greater availability of perches in the males' territory.

Hovering and flush-flying enable females to hunt in areas without perches, but at an expense of 8-12 times more energy used than for perch hunting (Lefebvre 1964, Tucker 1968). Females, therefore, expend a greater amount of energy during hunting than males.

Consumption of prey. – Analyses of variance showed no significant differences in the number or weight of prey taken per hour of observation by male versus female kestrels when considering the total quantity of invertebrates, mammals and birds (Table 2).

Table 2: Prey items eaten by male and female kestrels in California.

Kestrel sex		Invertebrate		Mammal		Bird		Reptiles		Unknown Vert.		Total hrs Observed
		N	Wt(g)	N	Wt(g)	N	Wt(g)	N	Wt(g)	N	Wt(g)	
Male	A	82	24.6	0	0.0	0	0.0	0	0.0	0	0.0	23.2
	B	96	28.8	1	10.0	3	30.0	0	0.0	0	0.0	38.8
	C	207	71.7	2	16.3	4	47.6	0	0.0	0	0.0	74.1
	D	148	44.4	9	66.2	3	30.0	0	0.0	0	0.0	56.5
	E	201	63.8	0	0.0	0	0.0	0	0.0	0	0.0	35.6
		734	233.3	12	92.5	10	107.6	0	0.0	0	0.0	228.2
Female	A	77	22.0	0	0.0	3	30.0	0	0.0	0	0.0	24.4
	B	98	19.6	4	33.1	3	68.7	1	0.0	1	10.8	44.5
	C	204	50.5	8	90.4	10	109.7	0	13.0	0	0.0	88.4
	D	148	29.6	10	129.4	1	10.0	1	10.0	1	21.5	51.9
	E	189	41.3	4	40.0	5	42.2	1	0.0	1	10.0	51.6
		716	162.0	26	292.9	22	260.6	3	23.0	3	42.3	260.8

The weight of the vertebrate prey item represents only the amount of the prey that was eaten during observations.

Number of invertebrates/hr., $p = 0.40$; weight of invertebrates/hr., $p = 0.70$; number of mammals/hr., $p = 0.26$; weight of mammals/hr., $p = 0.18$; number of birds/hr., $p = 0.09$; weight of birds/hr., $p = 0.06$.

Table 3: Total amount of vertebrate prey taken by individual kestrels.

Sex	Kestrel	Total vertebrate prey	
		N	Wt(g) ^a
Male	A	0	0.0
	B	4	40.0
	C	6	63.9
	D	12	96.2
	E	0	0.0
Total		22	200.1
Female	A	3	30.0
	B	8	112.6
	C	19	213.6
	D	13	170.9
	E	10	92.7
Total		53	619.8

^a Calculated from the actual amount of the vertebrate item eaten during observation.

ANOVA, number of vertebrate prey/hr., $F = 6.48, p = 0.03$; weight of vertebrate prey/hr., $F = 6.36, p = 0.04$.

When comparing either total number or total weight of vertebrate prey taken per hour of observation by sex, females utilized significantly more vertebrate prey than males (Table 3). In Table 4 though, analyses by Student's t-tests showed no differences in the mean weight of mammal prey taken by either sex ($p = 0.10$), but a significant difference ($p = 0.036$) in the weight of the birds selected, with males preying on larger ones. Excluding the relatively large Brewer's Blackbird (*Euphagus cyanocephalus*), analyses continued to show a significant difference in the weight of birds chosen by the sexes.

A Chi-square analysis of mean number of insects/4000 m² in male and female territories indicates no difference ($p > 0.10$, Fig. 1). The number of birds and mammals in male and female territories are however, dissimilar (Chi-square analysis: birds/4000 m²; $p = 0.016$; mammals/4000 m²; $p \leq 0.005$; Figs 2 and 3). Females consumed more vertebrates in territories with high vertebrate density.

Success of predation. - Analysis of variance between hunting success of individuals indicates no difference between the sexes (Table 5). In addition, a comparison of monthly predation success between males and females using a Chi-square analyses on arcsine transformed data shows no difference ($p > 0.10$, Table 6). The sexes secured proportionately different numbers of vertebrates and invertebrates (Tables 2 and 3). Both sexes however, are equally successful in obtaining prey during the winter (female predation success, 36.4%; male predation success, 43.8%; Table 5).

Table 4: Mean weight of prey taken by male and female kestrels.

Prey	Weights (g)	Number		Total weight	
		Female	Male	Female	Male
Dragonfly	0.5	0	2	0	1.0
Beetle	0.1	1	0	0.1	0
Earthworm	0.3	0	6	0	1.8
<i>Stenopelmatus longispinus</i>	3.5	11	3	38.5	10.5
Unidentified invertebrates	0.2	676	721	135.2	144.2
Total invertebrates		688	734	173.8	157.5
<i>Spinus psaltria</i>	9.6	3	0	28.8	0
<i>Euphagus cyanocephalus</i>	56.9 ^a	0	1	0	56.9
<i>Passerculus sandwichensis</i>	18.4	1	0	18.4	0
<i>Carpodacus mexicanus</i>	21.7	4	2	86.8	43.4
<i>Zonotrichia leucophrys</i>	25.3	2	5	50.6	126.5
Unidentified birds	22.8	13	2	296.4	45.6
Total birds		23	10	481.0	272.4
<i>Thamnophis</i> sp.	20.0	1	0	20.0	0
Unidentified lizard	3.0	1	0	3.0	0
Total reptiles		2	0	23.0	0
<i>Microtus californicus</i>	33.3	9	0	299.7	0
<i>Sorex</i> sp.	6.0	2	0	12.0	0
<i>Peromyscus maniculatus</i>	12.6	6	1	75.6	12.6
<i>Mus musculus</i>	12.7	0	6	0	76.2
<i>Thomomys bottae</i>	32.0 ^b	0	1	0	32.0
Unidentified mammal	20.2	11	5	222.2	101.0
Total mammals		28	13	609.5	221.8

^a Mean weight of female *Euphagus*.^b Actual weight of *Thomomys* caught by male.Mean weight of identified birds taken, female \bar{x} = 18.5 g, N = 10; male \bar{x} = 28.4, N = 8.Mean weight of identified mammals taken, female \bar{x} = 22.8 g, N = 17; male \bar{x} = 15.1, N = 8.

Time and activity budgets of kestrels. – A Chi-square test indicates a significant ($p < 0.005$) difference between the sexes in the amount of time spent in separate activities (Table 7). Both sexes spent equal time actively perching and preening. Females however, used significantly less time inactively perching and more time hovering, flying, eating, fighting, and caching than males. Overall, females spent more of their time in energy expensive activities than males.

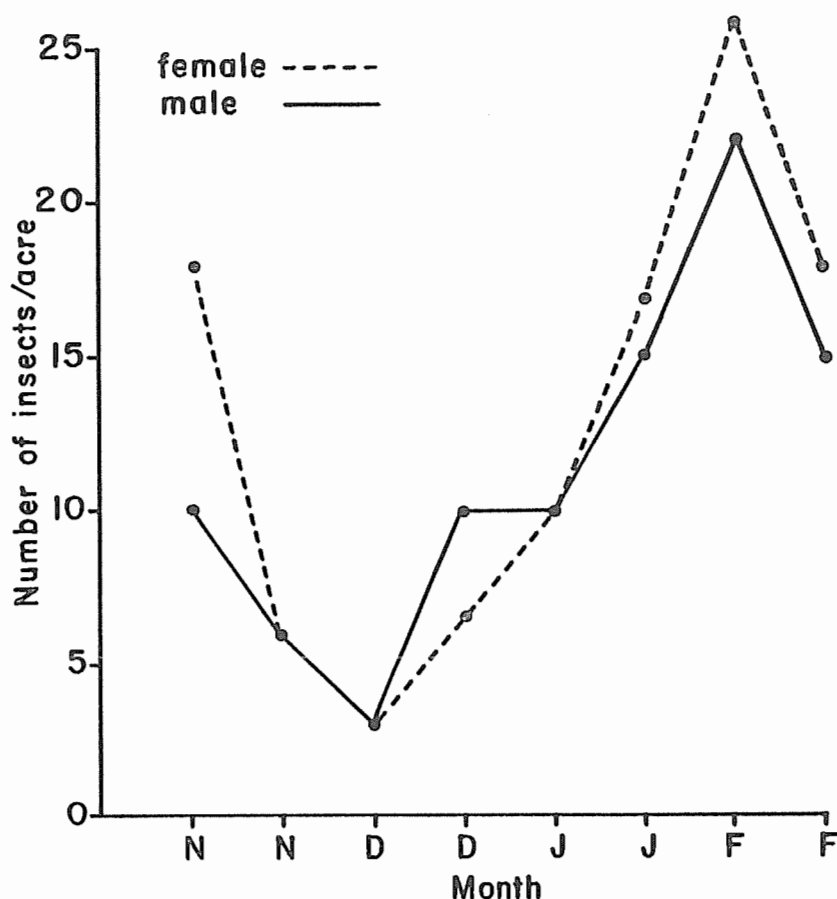


Figure 1: The mean number of insects in kestrel territories.

Female kestrels interact with avian predators nearly 70 percent of the encounter time, while males interact with predators only 16 percent of the time (Tables 8 and 9), respectively. Considering all interspecific encounters with other birds, female kestrels were more often on the offense (69.4 percent), while male kestrels spent only 30.2 percent of the time on the offense. Offensive actions by kestrels are more often directed against raptors than against all other birds. Females might have a higher mortality rate than males during winter due to this higher frequency of encounters by avian predators, namely Great Horned owls (*Bubo virginianus*), Golden Eagles (*Aquila chrysaetos*), Red-tailed Hawks (*Buteo jamaicensis*), and Prairie Falcons (*F. mexicanus*).

Wintering territories of kestrels. - Female territories contained 1.7 times more birds/4000 m² and 5.6 times more mammals/area than male territories. In addition, female territories averaged 2.4 times more area than male territories (territorial areas in hectares were 18.7, 21.4, 36.7, 39.1, 42.0, \bar{x} = 31.6, S.D. = 10.7 for females, and 9.7, 13.4, 13.7, 14.8, 14.0, \bar{x} = 13.1, S.D. = 2.0 for males). Females, therefore, have a greater number of potentially available prey than males.

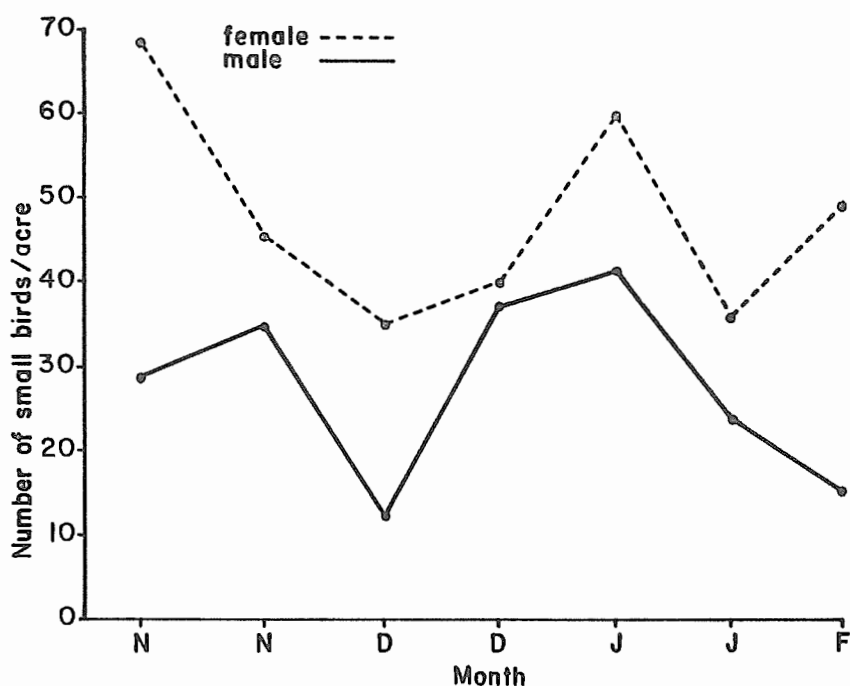


Figure 2: Counts of birds in kestrel territories.

Table 5: Success of predation for individual male and female kestrels during winter.

Sex	Kestrel	Success of hunting (%)	Total hours observed
Male	A	34.1	23.2
	B	36.6	38.8
	C	41.0	74.1
	D	46.9	56.5
	E	60.3	35.6
	Total	218.9 ($\bar{x} = 43.8$)	228.2
Female	A	37.4	24.4
	B	29.3	44.5
	C	34.5	88.4
	D	41.0	51.9
	E	39.7	51.6
	Total	181.9 ($\bar{x} = 36.4$)	260.8

ANOVA, predation success. $F = 2.73, p = 0.13$.

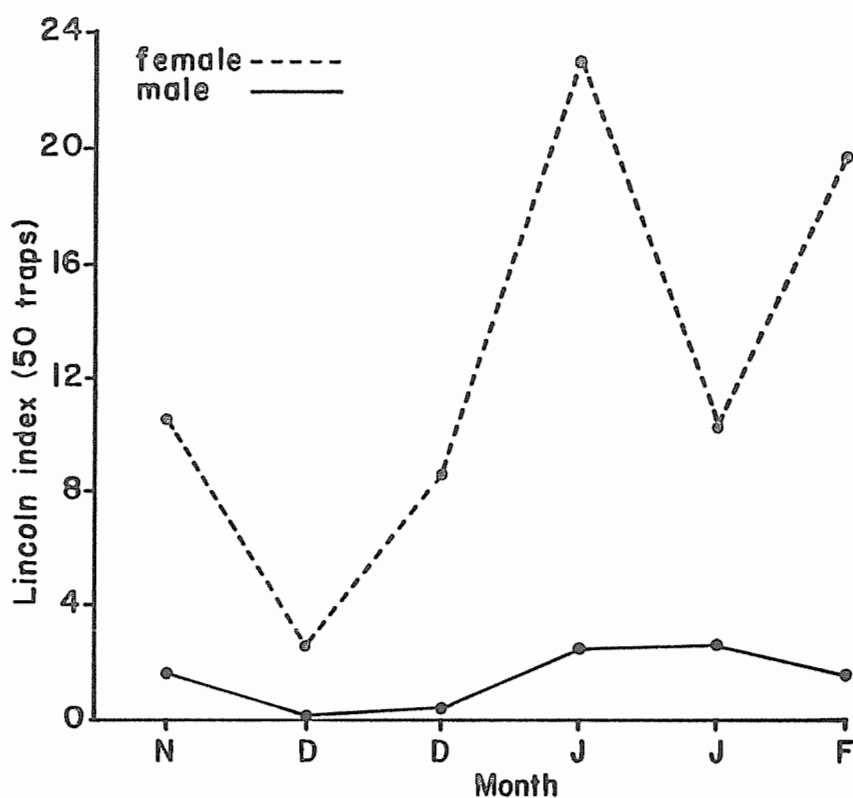


Figure 3: Counts of small mammals in kestrel territories.

Table 6: Comparison of monthly predation success between male and female kestrels.

Month	Female strikes		Hunting Success (%)	Male strikes		Hunting Success (%)
	Total	Successful		Total	Successful	
Oct	129	59	45.7	84	54	64.3
Nov	257	121	47.1	215	144	67.0
Dec	337	115	34.1	276	126	44.9
Jan	505	160	31.7	382	129	33.8
Feb	268	96	35.8	230	86	37.4
Total	1496	551	36.8	1187	539	45.4

Two-way ANOVA using arcsine transformation; difference between hunting successes of sexes, $F = 7.52, p = 0.10$.

Table 7: Time and activity budget for male and female kestrels in winter.

Activity	5 Females	5 Males
	Total time (min)	Total time (min)
Active perching	4831	4029
Inactive perching	7830	7584
Hovering	133	31
Flying	981	654
Preening	950	752
Eating	617	323
Fighting	36	14
Caching	51	20

Total observation time was 223.45 hrs. for males and 257.15 hrs. for females.

Chi-square test; active perching, $p = 0.057$; inactive perching, $p < 0.005$; hovering, $p < 0.005$; flying $p < 0.005$; preening, $p = 0.061$; eating, $p < 0.005$; fighting, $p = 0.011$; caching, $p < 0.005$.

The larger winter territory size of females may relate to: 1) the greater food needs of the female than the male, (see Mosher and Matray 1974), or 2) the necessity of a larger territory for vertebrate predation, or 3) sparse vegetation and few physical barriers. Greater numbers of available vertebrate prey represent more potential food for the female whose larger body mass and more strenuous activities might call for higher food requirements than those of the male. Females are approximately 1/10th larger by weight than males (Brown and Amadon 1968, Balgooyen 1976). Mosher and Matray (1974) found that the larger female Broad-winged Hawk (*B. platypterus*) required more total energy/day than the smaller male.

In addition to greater food requirements for their larger size, female raptors require energy for development of the ovary (Cavé 1968). Cavé reported that for Eurasian Kestrels (*F. tinnunculus*), oocyte development begins in September and continues throughout winter and spring. Natural selection may favor females that seek areas of high prey densities, which potentially furnish more food than areas of low prey densities.

Schoener (1968) stated that in general, territory size (eds. - he did not specify winter or breeding) increases as prey density decreases; however, he failed to correlate prey density with territory size in the falcons, *F. mexicanus* and *F. sparverius*. Schoener stated these "falcons are responding to some feature of their habitat related to demands of their hunting style". With kestrels, size of the winter territory may relate to the physical properties of the territory rather than prey densities per se. Recently, Bowman and Bird (1986) found a negative correlation of prey abundance and territory size of breeding kestrels. However, in our study, female kestrels ate 7.15% vertebrates by weight ($n = 53$), in contrast to males (3.04%, $n = 23$). Most small mammals and birds are territorially spaced, and therefore, a larger area may be needed to supply a female kestrel with prey. On the other hand, insects may be found in high density within a small territory.

Table 8: The amount and kind of interspecific encounters of male kestrels.

Species	N	%	Time (sec)	%	Interactions					
					Kestrel			Other species		
					None	Defense	Offense	None	Defense	Offense
<i>Buteo jamaicensis</i>	7	16.28	347	47.60			7		7	
<i>Sayornia nigricans</i>	1	2.33	5	0.68		1				
<i>Pica nuttalli</i>	1	2.33	13	1.78		1				1
<i>Corvus brachyrhynchos</i>	1	2.33	54	7.41		1				1
<i>Mimus polyglottos</i>	3	6.97	28	3.84	2	1				3
<i>Lanius ludovicianus</i>	14	32.55	135	18.52	8	6			7	7
<i>Sturnus vulgaris</i>	5	11.63	37	5.08	2		3		3	2
<i>Euphagus cyanocephalus</i>	11	25.58	110	15.09	7	1	3		4	7
Total	43	100.00	729	100.00	19 (44.2%)	11 (25.6%)	13 (30.2%)	0 (0.0%)	21 (48.8%)	22 (51.2%)

7 encounters with predators (16.3%).
 36 encounters with nonpredators (83.7%).

Table 9: The amount and kind of interspecific encounters of female kestrels.

Species	N	%	Time (sec)	%	Interactions					
					Kestrel			Other species		
					None	Defense	Offense	None	Defense	Offense
<i>Elanus leucurus</i>	3	6.12	32	2.86		1	2	1	2	
<i>Accipiter cooperi</i>	1	2.04	10	0.90			1		1	
<i>Buteo jamaicensis</i>	11	22.45	325	29.10		2	9		9	2
<i>Buteo lagopus</i>	6	12.24	125	11.19		2	4	1	4	1
<i>Aquila chrysaetos</i>	1	2.04	56	5.01			1		1	
<i>Circus cyaneus</i>	3	6.12	20	1.79		3		3		
<i>Falco mexicanus</i>	4	8.17	119	10.65		2	2		2	2
<i>Falco columbarius</i>	4	8.17	55	4.92			4		4	
<i>Charadrius vociferus</i>	1	2.04	24	2.15	1					1
<i>Sayornis saya</i>	1	2.04	7	0.63			1		1	
<i>Corvus corax</i>	1	2.04	11	0.98			1		1	
<i>Corvus brachyrhynchos</i>	2	4.08	51	5.57			2		2	
<i>Lanius ludovicianus</i>	9	18.37	276	24.71			9		9	
<i>Agelaius phoeniceus</i>	2	4.08	6	0.54	2					2
Total	49	100.00	1117	100.00	3 (6.1%)	12 (24.5%)	34 (69.4%)	5 (10.2%)	34 (69.2%)	10 (20.4%)

33 encounters with predators (67.3%).

16 encounters with nonpredators (32.7%).

A third factor that may relate to size of the territory may be the physical properties of the area. Miller (1931) found that Loggerhead Shrikes (*Lanius ludovicianus*) possess larger territories in areas of sparse vegetation and few physical barriers. Miller's description of the larger territory closely resembles the open territory occupied by female kestrels, while the smaller one approximates the male's closed territory.

An absence of trees or bushes characterized female territories. Trees and bushes located along roads, plots beside farm houses and buildings, and orchards were typical of male territories. A two-way analysis of variance between the types of habitats chosen by the sexes for hunting showed a significant ($f = 12.68, p < 0.01$) difference (Table 10). Grazed pastures represented 70% of the combined area of the territories of the 5 females. In the 5 males studied, grazed pastures, barley fields, fallow areas, and orchards were the primary hunting areas. The female spent 93.3% of the observed time hunting in plots with vegetative cover measuring less than 14.7 cm in mean height. This mean vegetative height represented 96.4% of the combined total area of the female's territories. On the other hand, males hunt only 53.5% of the time in vegetation of less than 14.7 cm which constitute 61.3% of the male's total area. Males, therefore, are utilizing other areas such as orchards (17.2% of the time), which are absent in female territories.

Such physical factors as a smaller body size and a lower wing loading (Brown and Amadon 1968, Balgooyen 1976), may allow the male to hunt more successfully than the female in areas with trees. Smaller body size and shorter wing length of the male compared to the female may allow easier movement through vegetation, and therefore, permit habitation in closed areas.

A Chi-square analysis of hunting success on various vegetative plots show female kestrels had similar success rates in 5 areas (shoulder of road, fallow area, and plowed fields) (Table 10). Females capture prey at lower rates in alfalfa and barley fields ($p < 0.005$). Males capture prey with similar success in alfalfa fields, shoulders of roads, barley fields, fallow areas, vineyards, walnut orchards, plowed fields, and roads. Males are significantly ($p < 0.01$) more successful in grazed pastures and are significantly ($p < 0.025$) less successful in harvested fields, and in apricot orchards than other areas ($p < 0.005$). Possibly, the concealment afforded by orchard cover or some other feature hunting success may be advantageous to male kestrels.

A hypothesis for habitat separation by kestrels. - Sexual differences within a species suggest mechanisms of natural or sexual selection which may result in spatial or temporal separation of the habitat (Willson 1970) or dissimilar natural histories (Selander 1966). Both behavioral and physical factors are important in habitat selection. On the one hand, the sexes may occupy slightly different habitats and show sexual monomorphism. This situation may be more prevalent along bird populations than previously thought, e.g., the Brown-headed Nuthatch (*Sitta pusilla*) studied by Norris (1958), and other examples in Morse (1980). Alternatively, in cases where the sexes possess different life histories in a similar habitat or live in different habitats, a sexually dimorphic species could evolve. Sexual dimorphism can also occur in species where the sexes express similar strategies and occupancy (see Morse p. 41, 1980). Since both natural selection, operating through intersexual competition, and sexual selection, manifested mainly through intrasexual competition, are possible, the causes of sexual polymorphism are difficult to ascertain.

Is it intersexual competition or preference that best explains the habitat separation by sex during winter? From an evolutionary viewpoint, the ancestor of raptors was probably monomorphic in size and color. For kestrel-like falcons, breeding occurred in relatively open habitats with nests placed on cliffs or earthen banks. For reasons of energetics, pairs with smaller males proved more successful than pairs with large males,

Table 10: Height and cover density of different hunting areas in relation to percent of total area and percent use of each area by male and female kestrels.

Hunting area	Height (cm) Mean \pm S.D.	Cover Density (%)	Area (sq.m.)		% Total plot		No. of strikes		% Total No. Strikes		Hunting success (%)	
			Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Grazed pasture	9.4 \pm 5.3 9.9 \pm 10.2 9.7 \pm 6.0 13.0 \pm 4.8 11.4 \pm 14.5	100.0 100.0 100.0 100.0 97.1	1095300(5)	82000(5)	69.6	11.7	735	438	42.6	29.8	41.1	52*
Alfalfa field	9.1 \pm 3.0	100.0	179500(2)	43700(1)	11.4	6.2	246	48	14.2	3.3	29.6*	31.3
Shoulder of road	10.9 \pm 13.0	100.0	23900(5)	15300(4)	1.5	2.2	469	82	27.2	5.6	36.6	46.2
Barley field	12.2 \pm 1.3	100.0	101300(4)	150000(3)	6.4	21.4	81	160	4.7	10.9	21.1*	38.3
Fallow area	18.0 \pm 12.7 27.9 \pm 29.7 52.1 \pm 31.2 53.6 \pm 19.1	96.4 48.5 55.2 57.7	30100(1)	152000(4)	1.9	21.6	88	370	5.1	25.1	40.9	43.0
Vineyard	29.2 \pm 50.0	100.0	0	15000(1)	0.0	2.1	0	4	0.0	0.3	—	—
Harvested field	34.8 \pm 30.2 14.7 \pm 12.2	21.5 19.0	24800(1)	14500(2)	1.6	2.1	29	62	1.7	4.2	34.8	26.1*
Apricot orchard	583.9 \pm 93.5 457.2 \pm 173.5	42.8 18.2	0	38000(3)	0.0	5.4	0	185	0.0	12.6	—	28.6
Walnut orchard	605.5 \pm 48.5	47.0	0	52700(1)	0.0	7.5	0	67	0.0	4.6	—	38.9
Plowed field	0.0 \pm 0.0	0.0	69700(3)	27500(3)	4.4	3.9	45	40	2.6	2.7	37.5	50.5
Road	0.0 \pm 0.0	0.0	48100(5)	111600(5)	3.1	15.9	34	15	2.0	1.0	63.9*	56.3
Total			1572700	702300	99.9	100.0	1727	1471	100.1	100.1	37.9	43.9

() Represents number of territories having this vegetative type.

* Chi-square test shows significant difference in hunting success.

hence the genesis of sexual size dimorphism (Balgooyen 1976). It is not unreasonable to assume that small males of a small species incurred high rates of predation in open areas. Consequently, there was a shift in residence by males to edge habitats for protection.

This spatial separation would require that the males attract females during the breeding season. In the kestrel, pre-mating behaviors act to "orient" the female (see Balgooyen 1976). Both the fact that the male precedes the female in sexual readiness, and her following of the male during selection of a nest site are possible consequences of the spatial separation of the sexes. It is probable that sexual size dimorphism preceded, and was the cause of, both the shift into edge habitats and the development of sexual dichromatism. With time, male coloration became concordant with the features of the edge habitat. In essence, the male's coloration, low wing loading, small size, territorial maintenance, hunting techniques, etc. are geared to the edge habitat. Perhaps suffering less predation than the male, or being physiologically, or behaviorally suited, she remained in the "ancestral" open habitat.

Our study suggests that there is a "habitat split" rather than a "niche split" between the sexes of kestrels. The concept of the "niche split" was discussed by Selander (1966) and later by others, and implies that the sexes may, to reduce intersexual competition for food, select prey items which differ in behavior, morphology, physiology, and availability. If true, populations have been selected for more intense utilization of an area at high species density. On the other hand, a "habitat split" proposes that the cause(s) of dissimilar habitats is related to an advantage(s) for one or both sexes. The distinction being made here is predicated on the definitions of niche and habitat (see Whittaker et al. 1973). The "niche split" captures the functional aspect whereas the "habitat split" relates only to occupancy with different causes (Whittaker et al. 1975).

Koplin (1973) and Mills (1975) argued that habitat division by the sexes of kestrels is from intersexual competition. Koplin favors competition for food while Mills opts for female dominance as cause of habitat separation. Cade (1960), Collopy (in Koplin 1973), and Balgooyen (1976) reported the capture of similarly sized prey during the breeding season, thus supporting the competition theory. Mills (1976) found however, that male kestrels capture more birds than females. Our study showed that females took more vertebrate prey than males. We found a dissimilar distribution of prey in male and female territories which was reflected in the diet of each sex. Thus the differences in diet between the sexes appears to be a result, and not a cause of habitat separation. Furthermore, if males and females were splitting the niche, the sexes could coexist in either habitat.

Koplin conceded that the sexes should feed on prey which correlate to the size of the predator, but he further stated that kestrels are an exception because of low size sexual dimorphism. Morphometric studies of kestrels (Balgooyen 1976) revealed similar measurements of the "tools of predation" (beak, feet, claws) between the sexes, and that dimorphism appears to be primarily in terms of body weight. Kestrels are expected to feed on prey which correlate with their tools of predation and not body size (Balgooyen 1976). Deviation from similar diets by sex must relate to differing availabilities of prey. We found that wintering territories of kestrels differed as to prey quantities, and the sexes exploited prey in proportion to its availability. Likewise, both sexes used similar hunting techniques, but in different proportion. In other words, it is expected that kestrels will take prey items according to relative availabilities rather than sexual preferences (see also Mills 1975, 1976, and Balgooyen 1976).

If intersexual competition for food was operating between individuals with similar tools of predation, it is reasonable to expect occupancy of either sex in open or closed areas. Since this is not the case, does one sex dominate or outcompete the other or does

each sex select a preferred habitat? Mills (1976) argued that the female's larger size facilitates her dominance over the male. It should be noted that Koplin dismissed the sexual size difference in kestrels while Mills stressed it. Both however, contended that the female occupies the "best habitat". Occupation of a more favorable habitat should lead to differential survival and, therefore, a skewed sex ratio. From a review of the literature and observations in the field, Balgooyen (1976) reported a balanced sex ratio in populations of kestrels.

From the point of view of intersexual strategy, each sex likely selects a winter habitat that offers an advantage to individuals with different needs (see also Stinson et al. 1981). In essence, the separation of male and female winter habitats is a temporal-spatial consequence of the different breeding roles. Winter territories then, are established from intra- and not intersexual competition. Individuals in a species with sexual differences in coloration, wing loading, size, risk of predation, territory size, prey capture, and techniques adapt to particular habitats. Biological competition between the sexes is a rather poor ecologico-evolutionary strategy, but one found commonly between individuals of the same sex (Darwin 1871).

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THE ALLOCATION OF ENERGY IN THE ANNUAL CYCLE OF THE KESTREL, *Falco tinnunculus*

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Abstract: Using an empirical approach, the daily balance of energy intake and expenditure in free-living Eurasian Kestrel was examined as an intermediate link between behaviour and fitness. Three different methods of measuring energy expenditure, including doubly labeled water were used in field and laboratory. Over 700 days of continuous observation were collected on kestrels throughout their annual cycles for analysis of time and energy budgets.

A detailed analysis of time allocation patterns revealed the following: 1) At no time in the annual cycle was the whole daylight period devoted to intense foraging; 2) During reproduction, males maximized their daily energy gain by virtually exclusive flight hunting; and 3) The low-cost low-yield technique of perch-hunting is adopted in winter in association with flight hunting.

Measurements of metabolizable energy intake showed both daily and seasonal variation. Flight was the most expensive activity, but energy costs due to thermoregulation, moulting, and food intake were also significant.

The annual changes in the daily use of energy were constructed for male and female kestrels in terms of reproduction, moult and thermoregulation. The energetic consequence of alternative behavioural patterns are discussed.

The kestrel research project of the Department of Zoology at Groningen aims to evaluate the evolutionary benefits gained by individuals through the temporal order in their behaviour. Following the departmental research tradition, which originated with the work of the late L. Tinbergen and carried on by R.H. Drent, we have taken an empirically rather than theoretically based approach to the problem of temporal organization. While behavioural ecology is maturing as a respected branch of science, its skeleton of theory often outgrows the flesh of empirical data. Frequently, the question "how should an individual behave?" is posed and the answer then compared with reality. Our approach has been to quantitatively describe the real situation first and then to ask what the consequences of alternative strategies would be.

Such consequences should eventually be measured in the currency of reproductive fitness. However, the relationship between behaviour and fitness is rarely immediate. The work we summarize here, which formed the basis of the Ph.D. dissertation of one of us (D.M.), therefore investigated the daily balance of energy intake and expenditure in free-living kestrels as an intermediate link. This choice is based on the consideration that the daily energy balance on the one hand will reflect short-term results of behavioural decisions, and on the other hand affects survival and hence, reproductive prospects. The project extends the earlier research of Wijnandts (1984) on the nocturnal Long-eared Owl (*Asio otus*) to its diurnal counterpart as a vole hunter, the Eurasian Kestrel. This intermediate-sized bird combines good visibility with an overseeable home range (in the order of 400 hectares). A broad background of knowledge had already been assembled by Cavé (1968). In the earlier stages of the project we analysed the daily organization of hunting and feeding (Rijnsdorp et al. 1981) and its consequences for energy expenditure and reproductive perspective (Daan and Aschoff 1982).

The choice of the kestrel as the subject for this research was primarily determined by the methods to construct the balance of energy. For measuring the intake of energy

several possibilities exist. The most direct one is the assay of gross food intake by observation in the field. This can be translated into net energy intake if the energy content of the food and the assimilation quotient are known. The kestrel is an ideal species for applying this method. At least in our area, the bird has a simple diet, consisting of 92% Common Vole (*Microtus arvalis*). These are easy to collect in the hunting areas.

The study area is a recent land reclamation area and an open landscape, where individual kestrels can often be observed from dawn to dusk, and their meals can readily be observed. Kestrels further easily adjust to conditions of captivity, where assimilation of their natural food can be measured.

Energy expenditure of free-living birds can be assessed in one of 3 ways (Gessaman 1973). The time-energy budget method (TEB) is applicable to the kestrel since its behavioural modalities are easily distinguishable and continuous observations of focal birds are possible. The second method estimates CO₂ production from the differential turnover of deuterium and oxygen-18 in doubly labeled water injected into the body (DLW method; Lifson and McClintock 1966, Nagy 1980). A prerequisite for this method is that the animal can be reliably recaptured within a relatively short interval, one or two days. Since the kestrel is easily accustomed to breeding in nestboxes, and in our area also occupies these as night roosts, the method could be applied with some success. In order to find out whether the DLW would generate a figure for energy expenditure of the kestrel comparable with more traditional techniques, we did a number of measurements in the laboratory with simultaneous analysis of gaseous CO₂ production, assayed either gravimetrically with CaSO₄ absorption or by infrared gas analysis (Fig. 1). The average difference with the 2 assays was +2.2% (s.d. 5.0; n=8). For the third method, the net energy intake in the field served as a basis. If we can estimate which part of the energy intake is retained in the body, or which part of a possible energy store is mobilized, overall energy expenditure can be calculated. Such information can be derived from a detailed knowledge of body mass changes of females and males throughout the reproductive cycle.

Time allocation. - The data base for the analysis of time and energy budgets, as well as for the daily energy intake, comprised over 700 days of continuous observation of focal birds in the Lauwersmeer area. These were collected throughout the annual cycle. The behavioural protocol is schematically indicated in Fig. 2. Also, we sampled the food availability by a bimonthly snap trap census of the Common Vole population. However, it turned out that such trapping indices are not a reliable guide to food availability, since trappability of voles in spring during the growth of fresh vegetation is lower than otherwise, and since high vegetation and increased nocturnality of the voles reduced their availability to kestrels later in summer. A more straight forward measure of food availability is the yield of flight-hunting (i.e., the number of voles caught per hour by hunting kestrels). The average yield of hunting increases from 2.2 voles per hour in winter to 4.7 in summer (Fig. 3). We observed a decrease in August, which probably reflects a reduced hunting capacity of the kestrels while moulting. The seasonal variations in yield are primarily the consequence of an increase in vole densities during reproduction in spring and summer and of vole mortality in winter. These variations are essential for a functional analysis of the annual cycle and also for our understanding of the daily strategies in summer and winter.

The average time allocation during the various phases of the reproductive cycle is indicated in Fig. 4, for males and females separately. Both sexes in winter spend about 1.5 hours per day airborne, directional and hunting flight combined. Hunting flight includes both windhovering and short flights between consecutive windhovering positions. During courtship (phase 3) and egg-laying (phase 4) the female virtually stops

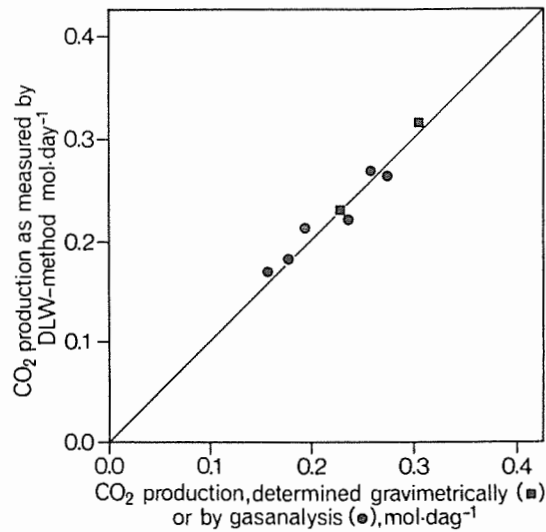


Figure 1: Carbon dioxide production of resting kestrels as measured gravimetrically and by infrared gas analysis, synchronously with the DLW method.

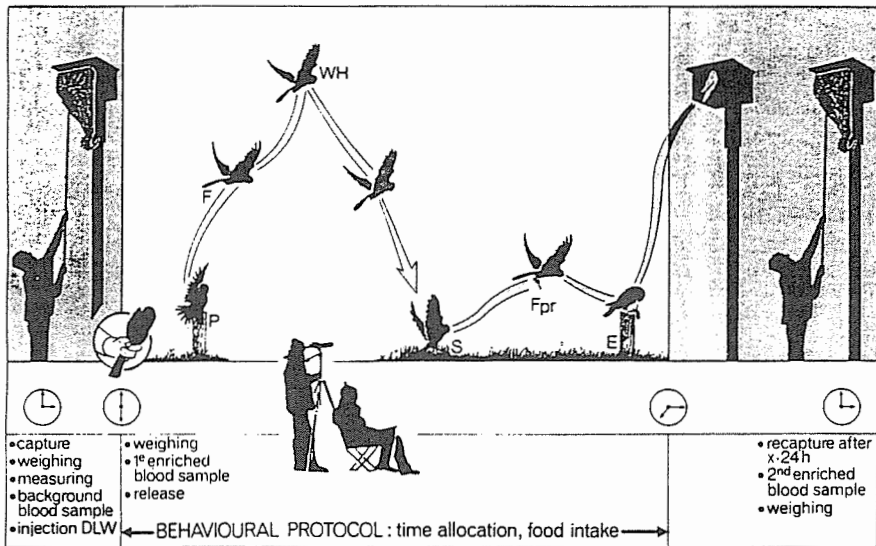


Figure 2: Diagram of methods used during observations of free-living kestrels. 1) Behavioural protocol: during the whole active period of the kestrel we made a behavioural protocol and registered each shift in behaviour to the nearest second. We distinguished: sitting in different positions, perching (P); sitting low (SL), sheltered (SS) and in the nestbox (SB); Flight (F) sometimes with prey (Fpr); Flight hunting (FH) sometimes interrupted for a strike (S), an attempt to catch a vole. In case of a prey capture eating (E) follows, alternatives are caching of the prey or prey transfer to female or nestlings. 2) Measurement of energy expenditure by means of the DLW-method, sometimes combined with a

behavioural protocol: after capture we took a background blood sample, and injected the bird with doubly labeled water D2180. After 3 hours, when the isotopes are equally distributed over the body water, we took a first enriched blood sample. After 24 hours, or a multiple of 24, we recaptured the bird and took a next blood sample.

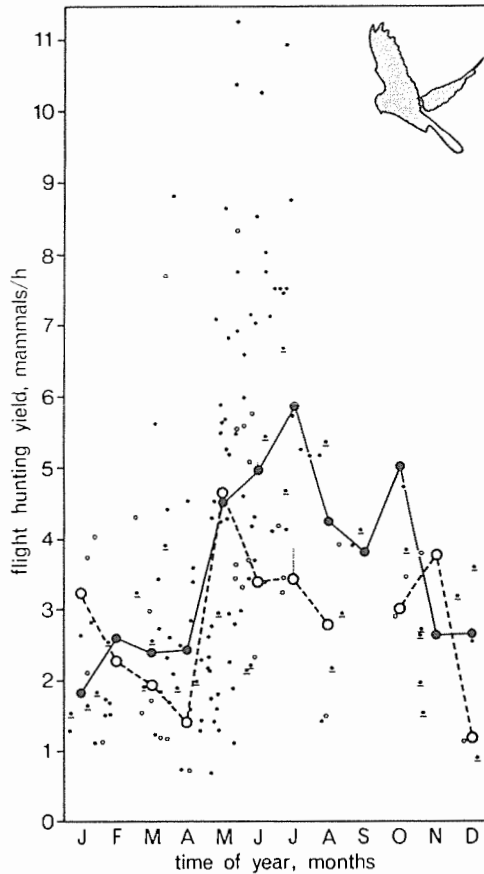


Figure 3: Seasonal variation in flight-hunting yield (mammals/hour) for males (O) and females (0) over the years 1977-1984. Small dots indicate flight-hunting yield of individuals observed for one or several days with at least 1 hr of flight-hunting. Underlined dots are from one individual male (#111). Large symbols indicate monthly mean yields (total no. of mammals divided by total hours flight-hunt). Vertical lines above monthly means are yield increments in birds caught per hour.

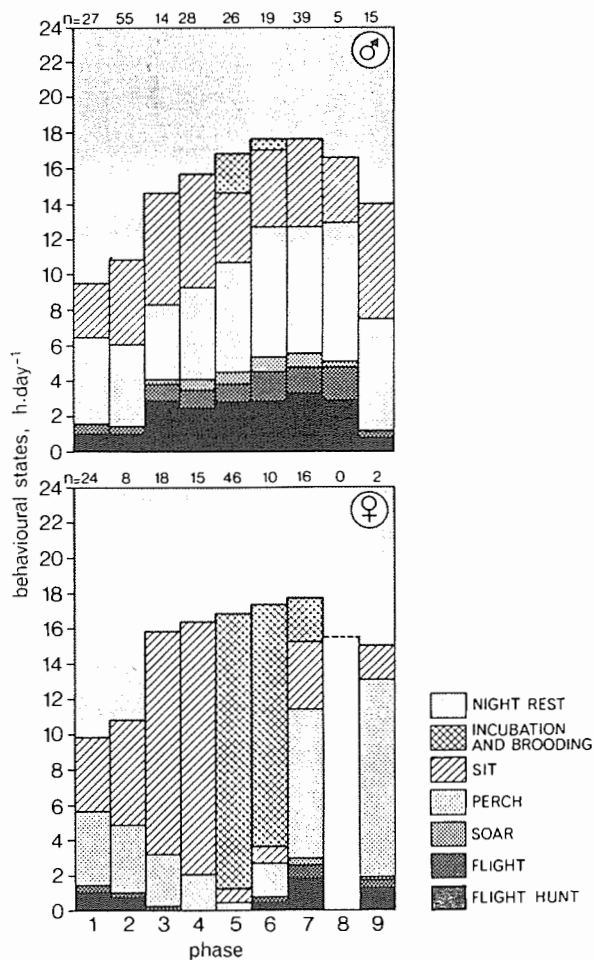


Figure 4: Variation with phase of the reproductive cycle in the allocation of time to different behavioural states in male (upper) and female (lower). Active day and night length were derived from monthly averages of times of departure from the night roost at dawn and of arrival of the kestrel at the roost at dusk (Masman 1986). Proportions of diurnal behaviour were derived from all complete observation days per phase (n). Phases: phase 1: winter unpaired; phase 2: winter paired; phase 3: courtship feeding; phase 4: egg-laying; phase 5: incubation; phase 6: nestlings < 10 days; phase 7: nestlings > 10 days; phase 8: fledglings; phase 9: post-reproductive moult.

flying, as she is being provisioned by the male. Males show a slight increase in hunting behaviour from courtship through incubation (phase 5), early and late nestling phases (phase 6, 7), and when nourishing fledglings (phase 8). Hunting is obviously reduced again in both sexes during moult (phase 9). At the time of maximum effort, during the late nestling phase, male kestrels on average do not work longer than 4.6 hours per day.

A detailed analysis of the time allocation patterns (Masman 1986) led to 3 general conclusions:

1) There are no circumstances, in the course of the annual cycle, under which the whole daylight period is devoted to intense foraging. This contrasts with the "stringency hypothesis" of Wilson (1975), which postulated that time budgets are evolved in adaptation to stringent periods in the life cycle of animals, during which food availability is so low (winter) or food demand so high (summer) that continuous foraging would be necessary.

2) During reproduction, males maximized their daily energy gain by virtually exclusive flight hunting. The total time spent airborne per day is presumably constrained by a limit to the amount of food which can be digested per day (Kirkwood 1983). If more energy is expended, body reserves will have to be combusted. We presume that long-term operation at or above this physiological maximum will reduce parental survival prospects (Drent and Daan 1980).

3) The low-cost low-yield technique of perch-hunting is adopted in winter in association with flight hunting. The preference for perch-hunting is incompatible with either of the 2 principles of time minimizing and energy maximizing (Schoener 1971, Norberg 1977). These strategies would both predict that flight hunting is used exclusively in winter, since flight hunting both minimizes the daily foraging time and maximizes the daily energy intake. The data seem only compatible with cost minimization, as in other non-reproducing birds (Gill and Wolf 1975).

Energy intake. - Figure 5 schematically shows the parameters to be measured for a complete understanding of the balance of energy. The daily energy intake was again derived from the field observations. We established the relationship between meal size and meal duration, making use of the fact that kestrels often cache their prey (Rijnsdorp et al. 1981). By weighing the cache and later watching the kestrel retrieve and eat it, we found that the meal size is approximated by $0.64 \cdot t^{0.59}$ g, where t =meal duration in seconds. By timing meals in the field using stopwatches we could estimate

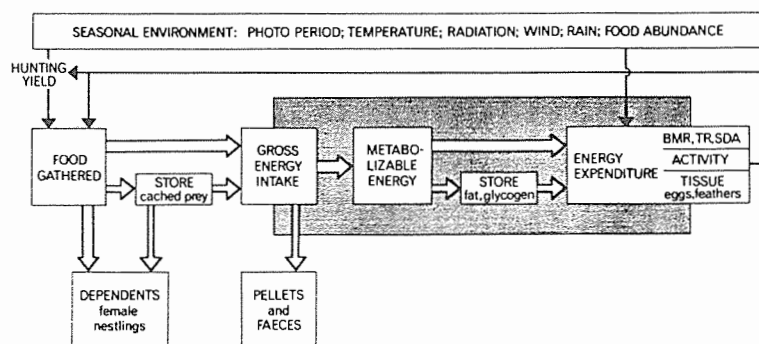


Figure 5: Diagram of the energy budget of the kestrel and main pathways for effects of seasonal variation in the environment on energy intake and expenditure.

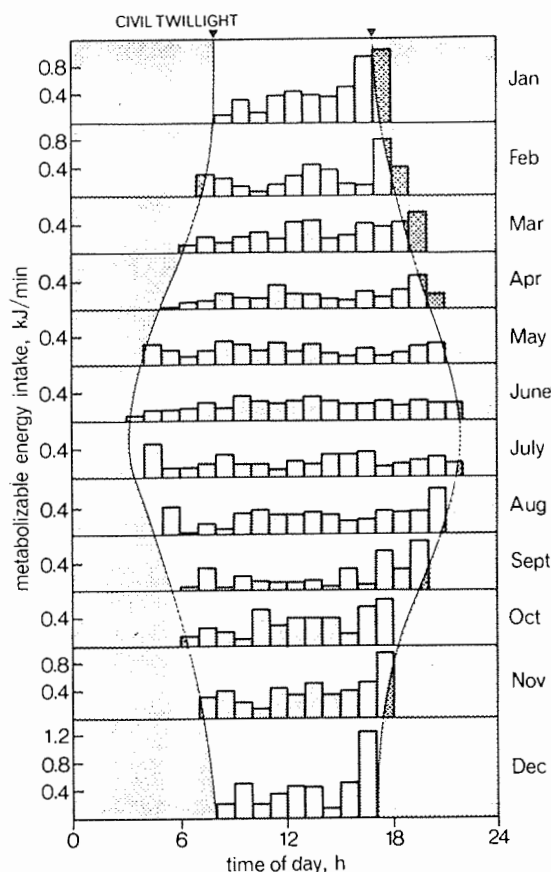


Figure 6: Variation of metabolizable energy intake (kJ/min) with time of day. Data for all complete observation days combined per month, except those for females during courtship feeding, egg-laying, incubation of brooding small nestlings (phases 3, 4, 5 and 6). Bars indicate mean energy intake in each hour interval (total observed energy intake was divided by total observation time). Shaded area indicates nocturnal rest.

prey mass in about half of the cases (922 out of 1944 meals). For the remainder of the prey, we applied size estimations specific for kestrel sex and time of year, since male kestrels bring larger prey to the nest than they eat themselves (Masman et al. 1986). In order to derive metabolizable energy intake from meal size and frequency, we measured prey energy content and, for the assimilation quotient Q , the energy content of feces and regurgitated pellets in laboratory trials with captive birds. Q varied from 65% (Common Shrews, *Sorex araneus*) to 75% (juvenile birds) and from 67% (winter voles) to 70% (summer voles). These figures eventually led to a reconstruction of the average metabolizable energy intake (M) per hour of the day (Fig. 6). From August till April there was a peak energy intake around sunset. This is partly achieved by caching prey in daytime and retrieval by the end of the day (Rijnsdorp et al. 1981). This behaviour keeps body mass low in daytime and hence also reduces the energetic costs of flight.

Further energy savings may arise from using the heat increment of feeding for nocturnal thermoregulation (Daan and Aschoff 1982).

The overall energy intake varies in the course of the year. Females have a peak intake rate of 371 kJ/day during egg-laying, which is 35% above winter levels. For males, the maximum was in the nestling phase (416 kJ/day): 52% above winter values. Metabolizable energy intake dropped to minimal levels during moult (August) in both males and females. The kestrel adjusts to seasonal highs in energy demand in several ways. In addition to increases in its food intake, it stores body reserves in advance, to be mobilized during demand peaks, and varies allocation to thermogenesis, reproductive activity and plumage repair sequentially (Masman et al. 1986).

Flight costs. – For the reconstruction of daily energy expenditure from time budgets it was necessary to measure energetic costs associated with various behavioural states. Flight is the most expensive action. We performed 2 types of experiments. In the laboratory flight costs were measured in trained kestrels. By varying daily flight distances (in multiples of 100 m), and simultaneously measuring energy intake, body mass change and O₂ consumption during rest between daily flight sessions, flight costs could be estimated, at 13.8 Watt (s.d. 3.1). Energy expenditure during directional and windhovering flight combined was measured in free-living birds. Using the doubly labeled water technique, overall energy expenditure was established in 10 individuals over a period of 1 to 3 days each. The birds were observed from dawn to dusk, and energy expenditure could be regressed on the fraction of time spent in flight (Fig. 7). From this relationship we estimated flight costs in the field at 14.6 Watt (s.d. 2.1). The correspondence between the 2 estimates led to the conclusion that one cost factor may be applied to both directional- and windhovering-flight. This value (14.6 Watt) corresponds reasonably with the prediction (15.1 Watt) from a new allometric equation relating flight costs dimensions (Masman and Klaassen 1987).

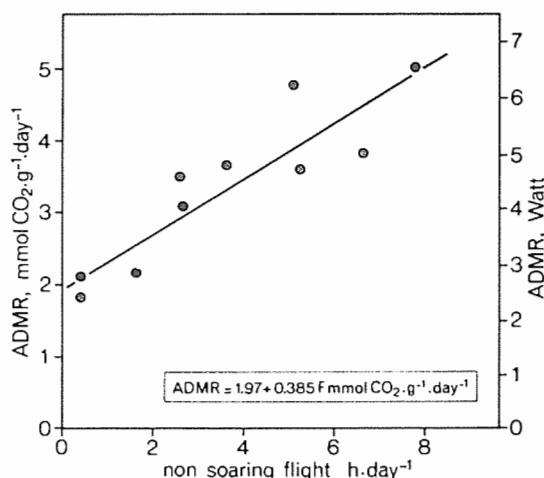


Figure 7: Average daily metabolic rate (ADMR) as a function of daily time spent in non-soaring flight. ADMR expressed in mass specific CO₂ production as measured by means of DLW, and as energy expenditure per bird (mean body mass = 213 g) using an energy equivalent of 0.528 kJ/mMol CO₂. Each dot represents one experiment lasting for at least 22 hours.

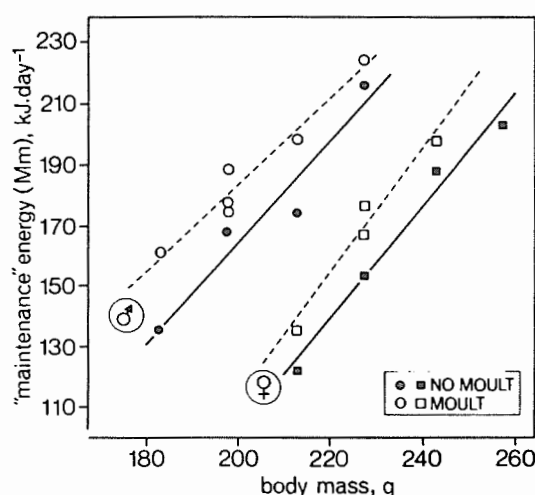


Figure 8: Energy required for maintenance (M_m) as a function of body mass for moulting (open symbols) and non-moulting (closed symbols), males (circles) and females (squares). Lines were calculated by linear regression.

Other costs. - Energy expenditures during other behaviours than flight were derived basically from a series of measurements of the oxygen consumption of tame trained kestrels sitting in various circumstances. In addition, we recorded daily metabolizable energy intake and body mass change in a number of captive kestrels through the annual cycle. As a starting point for the calculation, we used a basal level of metabolism (B), being the minimal O_2 consumption of resting, non-fed kestrels both in daytime and at night. There was a marked difference in these values between males and females. Males spent 12% more energy in basal conditions than females of the same body mass. The second component is the cost of thermogenesis at sub-thermoneutral temperatures. This was measured by the oxygen consumption of moulting and non-moulting birds over a range of temperatures. Moulting birds require 58% more energy for thermoregulation than non-moulting birds due to the impoverished insulating capacity of their plumage (Masman 1986). In order to apply thermoregulatory costs for field conditions, we used heated taxidermic mounts (Bakken et al. 1981, Buttemer 1985) to establish the combined effects of temperature, wind and radiation on heat loss.

The third component is the energy expenditure due to food intake: the heat increment of feeding (H). Kestrels turned out to lose 16.6% of their metabolizable energy intake in digestion. Part of the extra heat produced, in the order of 50%, appeared usable for thermogenesis. The fourth component is the cost of plumage synthesis during moult. The increase in metabolic rate, measured either in fasting or after feeding, during daytime as well as at night, was related to feather production rate. Kestrels used 109 kJ per gram feather formed, in addition to 23 kJ retained in each gram feather. Therefore, they need 132 kJ/gram extra metabolizable energy. This relationship was also determined by recording the food intake of moulting and non-moulting birds required to maintain a certain body mass (Fig. 8): $125 + 23 = 148$ kJ/gram. These figures are 3 to 4 times lower than those measured in passerine birds (Walsberg 1983). The differences are possibly due to differences in diet (carnivorous vs. granivorous birds) or in body size (Masman 1986).

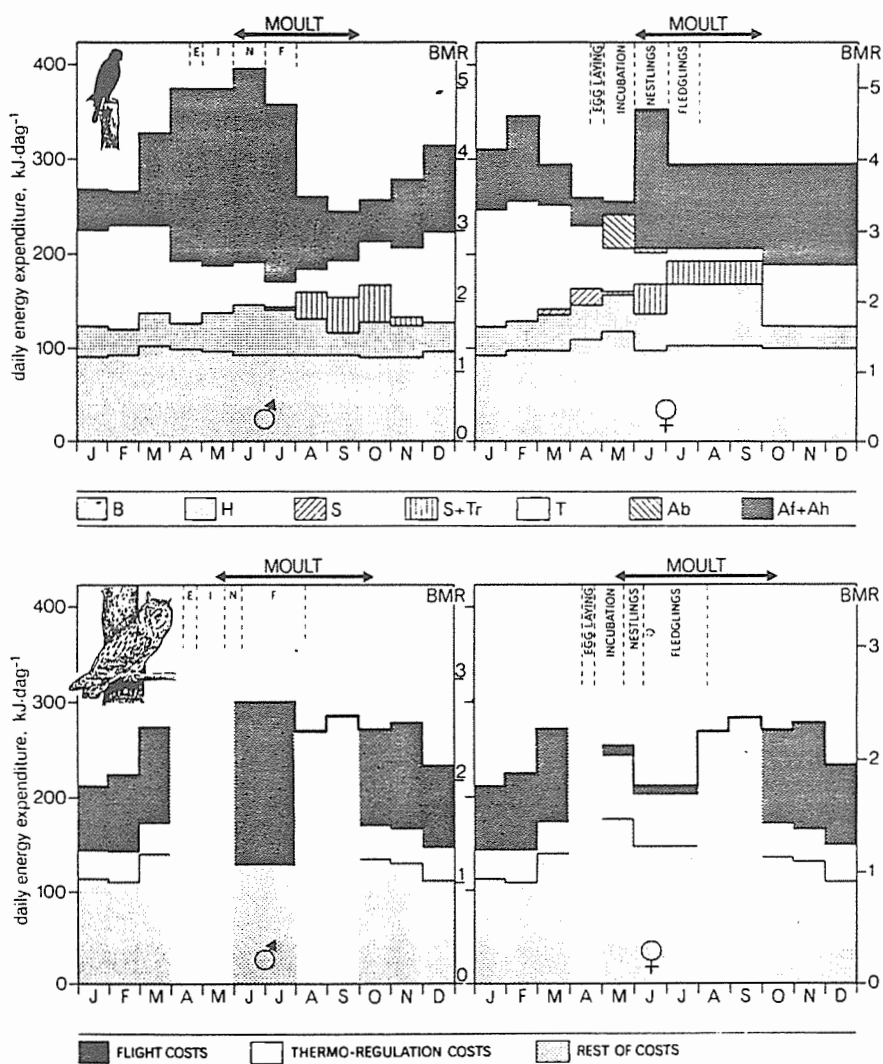


Figure 9: Annual variation in daily energy expenditure for male and female kestrels (upper) and Long-eared Owls (lower). Energy expenditure is partitioned in: B = basal costs; H = heat increment of feeding; S = egg synthesis; S + Tr = extra costs for moult: feather synthesis + extra costs for thermoregulation; T = costs for thermoregulation; Ab = costs for incubation; Af + Ah = costs for flight and flight-hunting. Data for the Long-eared Owl were derived from Wijnandts (1984).

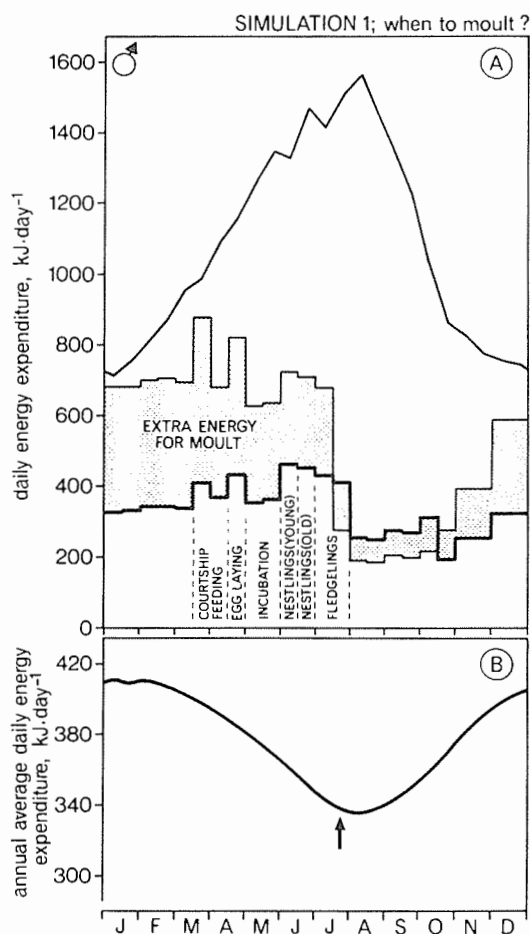


Figure 10: Simulated energetic consequences for a male kestrel of starting a moult period (3 months) in any of the 24 half- months of the year, given that the rest of the annual reproductive cycle is timed as it actually is. A: energetic consequences of moult in each half-month (dark area: extra energy expenditure due to moult). Line indicates the maximal energy expenditure, i.e., when full active day is devoted to flight. Heavy line indicates normal annual cycle. B: annual average daily energy expenditure as a function of start of moult. Arrow indicates the actual average moult onset in male kestrels.

Reconstruction of the annual cycle. – We integrated the different measurements by reconstructing the annual changes in the daily use of energy on the basis of the 3 methods described. We had 15 simultaneous measurements of daily energy expenditure by the DLW and TEB techniques. These independent estimates were significantly positively correlated, although TEB overestimated the DEE by 7%. Estimates for the average

DEE, based on metabolizable energy intake after correction for body mass changes are around 11% below those for TEB values.

The partitioning of energy expenditure, averaged per month for males and females, is illustrated in Fig. 9. The annual peak demand is for males during reproduction, at a time when females have their lowest expenditure. This clearly reflects task differentiation between the sexes. The seasonal variations in the energy budget are primarily due to the time used in flying and hunting. Part of these extra energy expenses during reproduction is compensated for by reduced costs of thermoregulation. The annual cycle resembles the picture (Fig. 9) obtained in the Long-eared Owl (Wijnandts 1984), which also feeds primarily on Common Voles. Males of both species have maximal rates of energy expenditure during reproduction while the females are at a seasonal low. In both, moult follows immediately upon reproduction, at a time when food availability is highest.

The analysis of energy expenditure patterns in the course of an annual cycle can provide indications about the constraints within which individuals can make their decisions. Having developed the equations relating the various components of the energy intake/expenditure budget to environmental variations, such as meteorological conditions and food availability, we can calculate the energetic consequences of alternative behavioural patterns. As examples, we computed the consequences of alternative timing of moult within the otherwise unchanged annual cycle and of alternative phase relationships between the annual cycle of the kestrel and its environment. Figure 10 summarizes how the mean daily energy expenditure would vary with altering the onset of the 3-month moult period. Kestrels start moult at the end of reproduction, at the highest temperature and just in advance of the peak in food abundance. Moult affects the energy budget by increasing the cost of thermoregulation and reducing the yield of flight hunting. Kestrels moult at the cheapest time of year, and small changes in timing, such as combining moult with reproduction, or moulting later in the autumn to allow extended care of fledged offspring, have important consequences for the average energy expenditure. Such considerations point to one of the disadvantages of late reproduction which most birds avoid in spite of the summer increase in vole abundance (Masman 1986). Further research by our group aims at an evaluation of individual strategies in annual timing and their impact on evolutionary fitness.

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ENERGETICS OF THE AMERICAN KESTREL IN NORTHERN UTAH

JAMES A. GESSAMAN and LUCINDA HAGGAS

Abstract: The energy metabolized daily by an American kestrel (*Falco sparverius*) is influenced by the air temperature, wind speed and solar radiation of its environment and by the energy requirements of fat deposition, growth, molt, flight activity, egg laying and incubation. Wind causes non-linear increases in kestrel metabolism as a result of wind penetration of the feather coat and exposure of the skin to forced convection processes. Solar radiation reduces metabolism of kestrels and extends their thermal neutral zone to lower air temperatures. Basal metabolic rate (BMR) and existence metabolism (EM) of kestrels are less than values predicted from standard equations relating BMR and EM to body weight of non-passerines. Kestrels living at 40°N latitude have a distinct annual cycle of body weight which directly reflects the annual cycle of body fat. The energy expended by male kestrels per day decreases from winter to spring. The energy metabolized by females in January is not significantly different from that in April; the energy cost of egg laying in April offsets the reduced costs of thermoregulation.

In this paper we have integrated the results of several laboratory and field studies of the energetics of the American Kestrel (*Falco sparverius*) in northern Utah. The temporal sequence of events in the annual cycle of the kestrel in northern Utah (Cache Valley) is shown in Fig. 1. We present data on the energy expended by a male and a female kestrel in carrying out some of these activities, as well as the seasonal changes in their daily energy expenditure (DEE). The DEE estimates have been derived from time budget studies of kestrels in the field combined with the rates of energy expenditure measured in the laboratory during different behaviors (flight and non-flight) and times of day (daytime and night time).

The DEE of the kestrel in northern Utah was computed for 3 different periods in a year: a non-breeding period (mid-January to mid-February), a breeding period (April through May, which includes the egg laying and incubation periods) and a post-breeding period (September).

METHODS AND RESULTS

Time budgets were derived from 18 free-living kestrels and 350+ h of direct observation utilizing the behavioral sampling techniques described by Altmann (1974). Single birds were observed from dawn to dusk with some half-day observations included. Observation hours were distributed fairly evenly among each season, sex and time of day to obtain a representative sample of kestrel activity. Male and female kestrels were each observed for approximately 60 h during each season. Kestrels had small home ranges (average maximum diameter = 0.97 km; L. Haggas unpubl. data) in open agricultural land and could be followed nearly all day. Elapsed time and hour (MST) of flight activities were recorded at close range from within a vehicle.

The DEE of a kestrel is the sum of the energy expended each day in metabolism (M_{24h}), plus the energy expended each day in tissue production (P). This is expressed by equation 1.

$$DEE = M_{24h} + P \quad (1)$$

American Kestrel Annual Cycle - Cache Valley, Utah

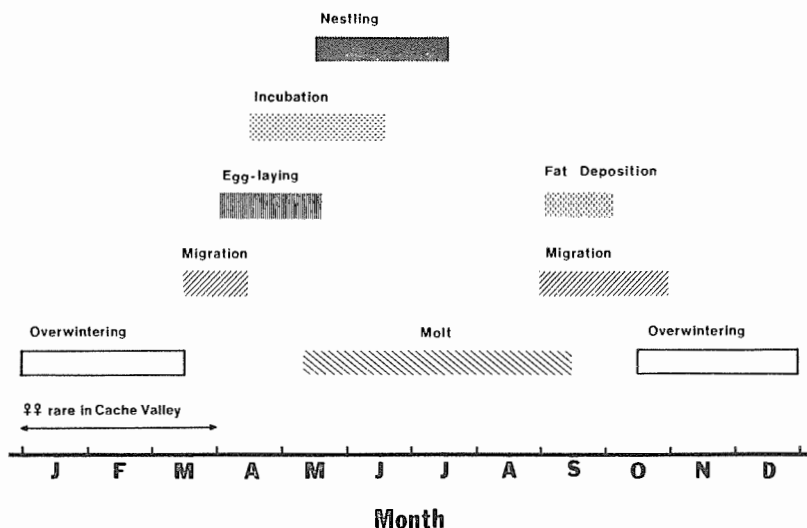


Figure 1: Events in the annual cycle of American Kestrels in northern Utah (Cache Valley).

Energy Metabolism. – Daily metabolism (M_{24h} , kcal/day) was calculated as a sum of energy metabolized during daytime flight and non-flight behavior and during night time rest. The method of calculating M_{24h} is shown in equations 2 through 7 (see Hayes and Gessaman (1980) for more detail).

$$M_{24} = M_{day} + M_{night} \quad (2)$$

where M_{day} = energy metabolized during the daylight hours and M_{night} = energy metabolized during the night.

$$M_{day} = NFEE + FEE \quad (3)$$

where $NFEE$ = energy expended during non-flight behavior (kcal) and FEE = energy expended during flight (kcal).

$$NFEE = t_{NF} \times NFMR \times W \quad (4)$$

where t_{NF} = the duration of non-flight behavior (h), $NFMR$ = the average metabolic rate during non-flight behavior (kcal/h/kg), and W = body weight (kg).

$$NFMR = 24.9926 - 48.9W - 0.3068T_a - 4.7724Q_s + 1.1688U^{0.5} \quad (5)$$

where T_a = ambient temperature (degC), Q_s = radiation flux density (cal/cm²/min) and U = wind speed (ms⁻¹).

$$FEE = t_F \times FMR \quad (6)$$

where t_F = the duration of flight behavior (h) and FMR = the average metabolic rate during flight (11.19 kcal/h for ; 12.68 kcal/h for ; Gessaman 1980)

$$M_{night} = (24 - t_{NF} - t_F) \times RMR \times W \quad (7)$$

where RMR = resting metabolic rate (kcal/h/kg) = $-0.264 T_{na} + 13.31$ (From Fig. 3 in Gessaman and Findell 1979). T_{na} = average night time temperature (degC).

The DEE analysis was completed with a 2-way analysis of variance (Cochran and Cox 1966). Variables included were: NFEE, FEE, M_{night} and DEE. Data were stratified by 2 factors (i.e., observation season [non-breeding, breeding and post-breeding] and the sex of the bird).

Energy Cost of Production. - Four types of tissue production occur during the 3 seasonal periods examined in this study, viz., growth of the gonads prior to the breeding season, egg production, fat deposition and molt.

The energy cost of gonadal growth equals the product of gonadal growth weight and energy content of the gonadal tissue divided by the energy efficiency of tissue growth. Gonadal recrudescence in males and females takes place over approximately 60 days. In males the left testis width increases from 2 mm in winter to 5 mm in mid-March to mid-May. In females the diameter of the largest follicle increases from less than 0.6 mm in winter to 3 mm in April. These growth rates require a daily rate of energy expenditure in males which is only 0.1% of their BMR (21.49 kcal/day) and a rate in females which is about 1.0% of their BMR (24.34 kcal/day; Gessaman 1980). In several avian species the energy cost of ovary and oviduct recrudescence has been shown to range from 2-13% of BMR (Ricklefs 1974).

The caloric cost of producing 1 egg is the product of the weight of the egg at laying and the caloric value of 1 g of egg divided by the caloric efficiency of egg formation. The energy cost of producing a clutch of eggs (EGPROD) is expressed in equation (8).

$$EGPROD = EGGS \times EGGWT \times CALEGG/EEP \quad (8)$$

Where EGGS = average number of eggs per clutch (4.5; A. Woyda unpubl. data); EGGWT = weight of egg at laying (15 g; R. Atkins unpubl. data); CALEGG = energy content of an egg (1.05 kcal/g; King 1973); EEP = efficiency of egg production (0.7; King 1973); and EGPROD = 101.25 kcal for kestrels.

These eggs are produced and laid over approximately 10 days (about 48 h between each egg). The daily energy cost of egg formation is therefore, 10.12 kcal/day or 41.6% of the BMR.

The energy cost of fat deposition equals the product of the weight of fat deposited and the energy content of fat (9.3 kcal/g) divided by the efficiency of fat production (0.6; Connell 1959). During an approximately 30-day period from 1 September to 1 October, male and female kestrels store 4.4 g and 8.5 g of fat, respectively (Gessaman 1979a,b). For males this daily cost is 2.3 kcal/day (10.6% of the BMR) and for females, 4.4 kcal/day (18.0% of the BMR).

Over a period of approximately 128 days from mid-May to mid-September male and female kestrels replace old feathers with 7.4 g and 8.4 g, respectively, of new ones. The energy cost of growing 1 g of feathers for a carnivorous bird at 17°C [average daily air temperature from May to September 1978 in Cache Valley, Natl. Climatic Center (NOAA)] is 41.3 kcal (Kendeigh et al. 1977). The average daily cost of molt for the male and female is therefore, 2.4 kcal/day (11.2% BMR) and 2.7 kcal/day (11.1% BMR), respectively.

Energy Cost of Incubation. - Gessaman and Findell (1979) found that the metabolism of female kestrels incubating in the field was only 2-5% higher than during a non-incubating period. These results are consistent with estimates and measures of the energy cost of incubation for other species which range from a 15% savings for incubating in well-insulated cup-shaped nests of 3 passerine species (Walsberg and King 1978 a,b) to 20-30% added cost for the Zebra Finch (*Poephila guttata*) (Vleck 1981) and the

Starling (*Sturnus vulgaris*) (Biebach 1977, 1979).

Energy Cost of Migration. - Band returns of kestrels banded in Cache Valley in the summer show that they migrate up to 2,500 km southward into Mexico for the winter. Migrating kestrels take advantage of thermals, tail winds and air deflecting upward from discontinuities in the landscape (i.e., mountain ridges). The estimated average rate of flight metabolism during migration (either northward or southward) is 4 times the kestrel's basal metabolic rate (1.014 kcal/h; Gessaman 1980). This estimate is based on 1) the long distance flight costs of passerines and pigeons (6 x BMR; Nisbet et al. 1963, LeFebvre 1964) and 2) the energy cost of gliding flight of birds (2-3 x BMR; Baudinette and Schmidt-Nielsen 1974).

We have flown kestrels in a wind tunnel at air speeds ranging from 10-50 km/h; the longest flights occurred at 40 km/h. At that rate a distance of 1,000 km could be covered during 25 h of flying time at a cost of 101.4 kcal. The fat reserves of males and females in October would only supply the additional energy required for a 403 km and 780 km migratory flight, respectively. Kestrels migrating from northern Utah to Mexico in the fall are undoubtedly feeding regularly during migration; many kestrels trapped by the first author during fall migration along the Goshute mountain ridge in eastern Nevada have had full crops. From a diet of a 20 g mammal a kestrel can assimilate 23.8 kcal of energy, therefore about 4 of these small mammals would supply the energy to fly 1,000 km.

Daily Energy Expenditure. - The DEE of a kestrel is significantly influenced by the season of observation and the sex of the bird ($p \leq 0.05$, Table 1). DEE is highest for non-breeding birds and lowest for post-breeding kestrels, while DEE levels during the breeding season overlap those from the other 2 seasons. Females have a significantly higher DEE than males.

Breeding females expended 10.34 kcal/day (42.5% of BMR) for reproduction which represents a significant ($p \leq 0.05$) addition to their DEE. The average costs of fat deposition and molt together account for 11.6% and 15.2% of the DEE for post-breeding males and females, respectively. These energy demands are a statistically significant ($p \leq 0.05$) addition to the DEE of post-breeding females, but not for males.

DISCUSSION

Daily Energy Expenditure. - The daily energy expended by kestrels varies seasonally, and generally the DEE of non-breeding birds is higher than that recorded from the breeding and post-breeding seasons. During the non-breeding season, kestrel weight is high, but air temperature (average daily and nighttime), and solar radiation are low; consequently, NFEE and M_{night} are correspondingly high. These meteorological conditions place increased thermoregulatory demands on kestrels during the non-breeding season and 91.3% of the DEE is the NFEE and M_{night} . This scenario is reversed during the breeding and post-breeding seasons as body weight is low and average daily and night time air temperature and solar radiation are high. Consequently, NFEE and M_{night} are low and account for about 75% of the DEE.

Female kestrels expend more energy for reproduction than males during the breeding season (which does not include the nestling period in our study) and for fat deposition and molt during the post-breeding season. These accrued costs of production for breeding and post-breeding females may elevate their DEE to that of non-breeding birds. DEE of non-breeding females is 0.5 and 9.7% higher than that of breeding and post-breeding females. In contrast, DEE of non-breeding males is 12-13% higher during the non-breeding season than the other 2 seasons. Apparently, males and females are mobilizing their metabolizable energy for those events that are the most demanding for

Table 1: Metabolism, production and daily energy expenditure (DEE) of kestrels during 3 seasons (see text for explanation) in northern Utah. Data are means followed by standard errors. W = body weight, t_F = time in flight, t_{NF} = time in non-flight, T_a = daily ambient temperature, T_{na} = night-time ambient temperature, Q_s = radiation flux density and U = wind speed. Units for metabolism and production are in kcal, DEE is in kcal/day.

Metabolism and Production = DEE												
								M_{day}	M_{night}			
	W (kg)	t_F (h)	t_{NF} (h)	T_a (°C)	T_{na} (°C)	Q_s (cal/ cm ² /min)	U (m/s)	NFEE	FEE			
Non breeding												
Males	.119	0.38	10.72	2.9	2.9	0.27	0.28	22.47	4.25	19.26	0.00	45.98 ± 1.12
Females	.138	0.33	10.77	2.8	3.2	0.25	0.28	24.99	4.18	22.19	0.00	51.36 ± 0.79
Breeding												
Males	.108	0.76	13.64	11.7	9.6	0.63	1.35	21.38	8.51	11.17	0.02	40.78 ± 1.85
Females	.124	0.34	14.06	11.8	9.3	0.63	1.33	23.52	4.31	12.92	10.34	51.39 ± 1.22
Post Breeding												
Males	.111	0.34	13.27	13.9	9.7	0.58	0.41	19.56	3.81	12.40	4.65	40.42 ± 2.99
Females	.127	0.42	13.18	13.6	11.9	0.59	0.39	20.96	5.32	13.43	7.11	46.82 ± 2.16

the season. Energy demands for thermoregulation decrease during the warmer months and kestrels may be able to mobilize energy more easily for tissue production at this time than during colder months. Females average 15.5% (17.2 g) heavier than males during all 3 seasons and expend slightly more energy for NFEE and M_{night} than males. Costs of production represent 42.5 and 30.8% of the females' BMR during the breeding and post-breeding seasons, compared to only 0.1 and 22.3%, respectively, for males.

FEE of breeding males is significantly higher than breeding females and non-breeding and post-breeding kestrels. This increased cost is related to a behavioral role change that has produced a division of labor within the nesting pair. Males have increased their flight activity levels to provision females (Haggas 1984), whereas females remain relatively sedentary in the vicinity of the nest, presumably conserving energy that is required for egg production.

Within the 3 seasonal periods examined in this study the DEE:BMR ratio for a kestrel in northern Utah ranged from 1.9 to 2.1 for males and females (Fig. 2). The highest ratios for both sexes occurred in mid-winter. A non-passerine bird the size of a kestrel should be able to daily assimilate and mobilize energy at a rate of 2 to 4 times its BMR (King 1973, Kendigh et al. 1977).

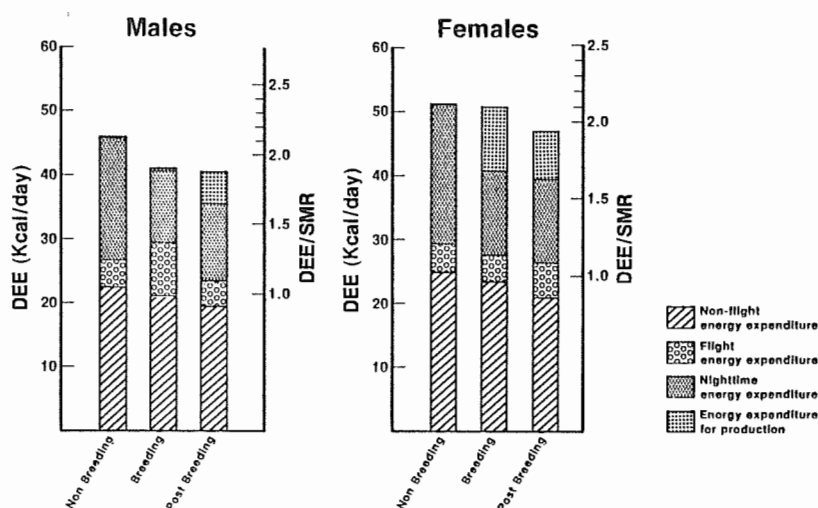


Figure 2: A partitioning of the daily energy expenditure (DEE) of male and female American Kestrels during 3 seasons in northern Utah and the ratio of DEE to basal metabolic rate (BMR). Non-flight energy expenditure = NFEE; Flight energy expenditure = FEE, Night time energy expenditure = M_{night} (see text for explanation of energy expenditure for production).

The upper limit of DEE is probably rarely or never experienced by kestrels wintering in northern Utah since 1) a DEE:BMR ratio of 2.1 reflects a DEE which is undoubtedly 25% or more below the maximum potential daily rate of the kestrel's energy expenditure, 2) more than fifty kestrels have been observed in mid-winter within approximately 10,000 ha of Cache Valley, Utah for several years (Gessaman 1982), and 3) kestrels regularly winter in regions that are colder and north of Utah (See Annual Christmas Bird Counts published in American Birds).

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DISPERSAL AND INBREEDING AVOIDANCE IN THE AMERICAN KESTREL: ARE THEY RELATED?

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Abstract: Data from 4 long-term kestrel banding projects were used to estimate rates of natal philopatry and adult site tenacity. Natal philopatry ranged from 1.5-3.8%. Juvenile females returned to their natal area more frequently, but considerably more females than males were originally banded. Adult site tenacity ranged from 9.7-22.6%. At Ste. Anne de Bellevue, Quebec, where the banding bias did not exist between sexes, males returned to their previous breeding areas more frequently than did females. Since the probability of detecting dispersal events is a function of the distance dispersed and the origin within the study area, the results suggest that American Kestrels (*Falco sparverius*) are loosely philopatric (within 8-10 home ranges). Since this likely acts as a passive mechanism of inbreeding avoidance, changes in local ecological conditions that disrupt dispersal patterns may adversely affect an evolutionarily stable inbreeding/outbreeding optimum.

Recently much attention has centered on the selective advantages of a small degree of inbreeding, often called optimal outbreeding (Bateson 1978, Shields 1982). According to the Optimal Outbreeding Hypothesis, selection for a mechanism preventing an individual from mating with a sibling should occur due to the high costs associated with incest (Bateson 1982). Complete outbreeding should also be selected against because of the breakup of co-adapted genomes. Thus a low level of inbreeding is optimal (Shields 1982). Shields (1983) suggested that philopatry has evolved as a means of achieving this low-level of inbreeding. Many mechanisms, both active and passive, have been suggested as ways to avoid extreme inbreeding. Greenwood et al. (1978) and Newton (1979) have espoused the theory that one function of natal dispersal is to reduce an individual's chance of breeding with closely related kin. Bateson (1978) has argued that behavioral avoidance mechanisms such as kin recognition serve to reduce the probability of extreme inbreeding. Whether active or passive, if the costs of extreme inbreeding are deleterious, some mechanism should have evolved to prevent its common occurrence.

Recent mate choice experiments in the laboratory have shown that behavioral avoidance mechanisms may serve to establish optimal levels of inbreeding. Bateson (1982) showed a significant preference for intermediately related individuals (2nd or 3rd cousins) over closely-related mates (brother or sister) in Japanese Quail (*Coturnix coturnix*), while Ratcliffe (1983) reported that Zebra Finches (*Poephila gutta*) preferred intermediate relatives over non-related individuals. American Kestrels (*Falco sparverius*) reportedly show no preference between mating with siblings or non-related individuals (Duncan and Bird 1987). If incest is more costly than complete outbreeding (Shields 1982), kestrels should have shown a preference for non-related individuals. The absence of a clear preference suggests that kestrels lack a behavioral mechanism, such as kin recognition, to avoid extreme inbreeding and implies that a passive mechanism may exist (Duncan and Bird 1987).

Kestrels are thought to be philopatric (Craighead and Craighead 1956, Smith et al. 1972, Balgooyen 1976), however none of the authors demonstrating philopatry used marked populations of birds. Under Mayr's (1963) definition, a conclusion of philopatry for American Kestrels might be premature, i.e., a high level of philopatry seems inconsistent in a species with no behavioral mechanism for extreme inbreeding avoidance.

The objective of this paper was to re-examine the degree of philopatry in kestrels using banding returns of wild, marked populations.

METHODS

Data were collected from 3 long-term kestrel banding projects conducted in St. Thomas, Ontario; Sharon, Connecticut; and Lassen County, California. Also, banding data collected from our own 4-year study in Ste. Anne de Bellevue, Quebec, were analyzed.

In all study areas, kestrels were migratory, except in California where certain valley kestrels are likely year-round residents (P. Bloom pers. comm.) and thus, excluded from the analysis. We considered a bird philopatric if it was retrapped within a 10 min latitude-longitude square from its initial trapping location during the breeding season (April-August), in any subsequent year. Where possible we differentiated between birds banded as nestlings and adults and between males and females. However, from 2 studies (i.e., Connecticut and California), we were provided simply with total birds banded and returned, which only permitted overall estimates of philopatry. At Ste. Anne de Bellevue, most adults on the study area were trapped and banded during the first year. During subsequent years, surveys were made of all known territories to search for returning birds. Some, but not all, new adults were trapped and banded. All young produced during the 4-year period were color-banded.

Since philopatric birds represent a proportion of those birds surviving to breed the next year and not the total birds banded, we reduced the total birds banded by an estimated figure representing annual mortality for juveniles (69%) and adults (45%) (Henny 1972). Hence, philopatry is represented as a proportion of surviving birds returning to breed within the square they were initially banded in.

RESULTS AND DISCUSSION

Natal philopatry (i.e., birds banded as nestlings returning to breed in their natal grid) ranged from 1.5 to 3.8% (Table 1). Cavé (1968) reported a juvenile return rate of 3.25% for Eurasian Kestrels (*F. tinnunculus*). Adult breeding area fidelity (i.e., adults returning to an area they had previously bred in and not a specific nest site) was considerably higher, ranging from 9.7 to 22.6% (Table 2). Cavé (1968) reported that 42.5% of female Eurasian Kestrels returned to an area where they had previously bred. However, if males are more site-faithful than females as has been found in other raptors (Newton 1978, Newton and Marquiss 1982), then this may be an underestimate of the total adult site fidelity. Overall philopatry rates from Sharon, CT and Lassen County, CA were 0.0% and 1.8%, respectively.

To demonstrate evidence of a passive mechanism of extreme inbreeding avoidance, sexual differences in natal dispersal patterns need to be demonstrated. Male natal philopatry ranged from 0-0.4% and female natal philopatry ranged from 2.7-7.3% (Table 1). These results were likely biased because adult females were much easier to capture than males. Although the sex ratio of banded juveniles was nearly 50/50, considerably more adult females were trapped than males (132 vs. 35). Possibly, a large percentage of returning males was undetected. At Ste. Anne de Bellevue, where the bias was minimized by complete yearly surveys of breeding birds, sexual differences in natal philopatry were far lower than at St. Thomas. Our small sample of natal returns however, made analysis of sexual differences in natal philopatry impossible.

Table 1: Estimates of natal philopatry based on returns of adult kestrels to within 218 km² of natal site.

Location	Sex	Total Banded	Survive to return ^a	Returns	% Philopatry
St. Thomas, Ontario		1375	426	16	3.7%
	Male	710	220	1	0.4%
	Female	665	206	15	7.3%
Ste. Anne de Bellevue, Quebec		218	67	1	1.5%
	Male	100	31	0	0.0%
	Female	118	36	1	2.7%

^a Based on estimated mortality rates of 69% and 45% for juveniles and adults, respectively (Henny 1972).

Table 2: Estimates of adult site fidelity based on returns of kestrels to within 218 km² of a previously used breeding site.

Location	Sex	Total Banded	Survive to return ^a	Returns	% Philopatry
St. Thomas, Ontario		112	62	14	22.6%
	Male	12	7	1	14.3%
	Female	100	55	13	23.6%
Ste. Anne de Bellevue, Quebec		55	31	3	9.7%
	Male	23	13	3	23.1%
	Female	32	18	0	0.0%

^a Based on estimated mortality rates of 69% and 45% for juveniles and adults, respectively (Henny 1972).

Sexual differences in adult site fidelity were somewhat ambiguous, however at Ste. Anne de Bellevue, males were considerably higher in this regard than females (Table 2).

Overall, American Kestrels appear to be less philopatric than has been suggested in the literature. However, the probability of detecting dispersal events is a function of the distance dispersed and the site of origin within the study area (Barrowclough 1978). Shields (1982) defined philopatry as returning to a site within 10 home-ranges from the natal site. Since most of these study areas were relatively small (i.e., 8-10 home ranges in diameter), many individuals could be philopatric by definition, yet not be recorded as returning to the study site. Our return rates indicate that kestrels are loosely philopatric, returning to the general area but rarely to the same site. Of 34 returning adults at St. Thomas and Ste. Anne de Bellevue, only 1 was known to have returned to the same nest.

Though Shields (1982) argued that dispersal patterns have evolved as a means of establishing optimal levels of inbreeding, Moore and Ali (1984) reported that the costs of excessive inbreeding or outbreeding have never been great enough to influence either dispersal patterns or behavioral mechanisms of inbreeding avoidance. Kestrels have large clutch sizes (relative to other raptors), low adult survival, and prey on cyclic, fluctuating prey species (Balgooyen 1976). Andersson (1980) developed a model which predicts that such patterns should favor the evolution of adult nomadism. Waser (1985) however, has demonstrated that high territory turnover rates should decrease the modal dispersal distance. Kestrel populations, characterized by nest-site limitation and high adult mortality, should exhibit high territory turnover. At Ste. Anne de Bellevue, the average lifespan of natural kestrel nest-sites was 1.8 years (R. Bowman unpubl. data); the ephemeral nature of cavity nesting in kestrels may offset the somatic benefits associated with philopatry and nest-site limitation (Balgooyen 1976). The results of opposing ecological selection pressures may have favored the loosely philopatric patterns we suggest for kestrels.

Greenwood (1980) argued that sexual differences in dispersal patterns depend on the individual mating systems of the species under consideration. Most raptors employ a male resource defence strategy; thus it is expected, and often shown, that females disperse more often than males (Newton 1979). Our results are, at best, equivocal about sexual differences in dispersal in kestrels. Recently however, Gonzalez (1986) examined kestrel band return data and concluded that males disperse less than females, but of those dispersing more than 100 km, there was no difference in the distance between the sexes. If sexual differences in dispersal separate closely-related individuals of different sexes, it would only be effective for short-range dispersal. Over longer distances, the low probability of random encounters would minimize selection for any separatory mechanism. Again, whether genetic or somatic factors influence the evolution of these patterns is ambiguous, however sexual differences in dispersal probably do serve as a passive mechanism for extreme inbreeding avoidance.

In all 13 recorded instances of close inbreeding in a pedigree wild population of Great Tits (*Parus major*) studied over a 10-year span, Greenwood et al. (1978) found that at least one member of each pair had an abnormal dispersal pattern. If loose philopatry is the normal natal pattern in kestrels, highly philopatric individuals may be more susceptible to high levels of inbreeding. At Ste. Anne de Bellevue, Quebec, only 1 of 218 juveniles returned to breed in the study area (Table 1). Interestingly, the female bred with its father and successfully fledged 4 young. This indicates support for Moore and Ali's (1984) contention that the costs of inbreeding are not excessively high. However, prolonged periods of extreme inbreeding should lead to inbreeding depression, or a decrease in the mean level of characters related to fitness (Falconer 1981).

Banding data from the 10-year nest box program in St. Thomas, Ontario, suggest that natal philopatry may increase after a period of intensive management has substantially increased the local populations. Increasing the number of nest boxes available to the local population effectively increases the turnover rate, and according to Waser (1985), decreases the modal dispersal distance. Managed nest box populations are likely to be denser than the dispersed populations characterized by natural cavity nesters. Denser populations would likely increase the interactions between individuals. If an increase in natal philopatry brings more related individuals into the local population, then intensive nest box management programs may increase local populations, but also increase the amount of inbreeding.

Conversely, unmanaged populations of American Kestrels may be faced with a similar problem. *Falco sparverius paulus* has been declining throughout its native Florida range during the last 100 years (Hoffman 1984). Destruction of breeding habitat, commonly singled out as the cause of the decline, may serve to disrupt dispersal patterns and concentrate surviving individuals in small areas of suitable habitat. If this subspecies does not have a behavioral avoidance mechanism, loss of habitat may be increasing the amount of inbreeding in an already small population.

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LINEAR AND WEIGHT MEASUREMENTS OF MATED PAIRS OF GREATER KESTRELS

ALAN C. KEMP

Abstract: Linear and weight measurements are presented for 23 male and 28 female Greater Kestrels (*Falco rupicoloides*) from the Republic of South Africa. Females were heavier and, on average, 2.2% larger than males, but males were larger than females in those dimensions related to prey capture (tomial tooth, anterior claw lengths and wing loading). All kestrels measured represented 32 mated pairs during the 8-year study. Comparison of measurements of members of pairs indicate little consistency in the direction of sexual size dimorphism for any one dimension. Seasonal variation in weight also appears to obscure any consistent differences between members of pairs.

Greater Kestrels (*Falco rupicoloides*) were measured and weighed for 3 reasons. First, detailed dimensions have not been recorded for either sex of this species. Second, there are no studies of raptors, to my knowledge, in which the dimensions of members of mated pairs have been compared; this is in spite of academic interest in the reversed sexual size dimorphism of raptorial birds (e.g., Newton 1979). Third, I intend to search for correlations between individual dimensions and lifetime reproductive success, in an attempt to determine which dimensions might contribute most to the biological fitness of an individual.

METHODS

Kestrels were trapped between 1975 and the end of 1983 on farmland near Pretoria, Republic of South Africa (Kemp 1978, 1984). Each kestrel was caught using a bal-chatri cage baited with laboratory mice. Up to 36 measurements, including weight, were recorded (Table 1), according to guidelines established by Biggs et al. (1978). Not all measurements were recorded for every kestrel, resulting in different sample sizes for each dimension in Table 1. Each kestrel was color-banded and released. Its sex and social position were recorded by observing subsequent interactions with other kestrels.

RESULTS

Linear measurements. – Measurements were taken on 23 male and 28 female adult or subadult (second year) kestrels. These individuals formed into 32 pairs which attempted breeding during the course of the study. Measurements for each sex and differences in measurements between members of mated pairs are shown in Table 1. On average, females were 2.2% larger than males in all dimensions (range 0 – 6.7%), except tomial tooth depth, anterior claw lengths and wing loading. There is however, overlap between the sexes for every dimension. Furthermore, when the dimensions of mates from known pairs are compared, the direction of sexual dimorphism is not constant for any dimension. This means that either mate may be the largest for a particular dimension and that no dimension is consistently different between the sexes.

Table 1: Measurements of male and female Greater Kestrels, and differences in measurements between mated pairs. Linear measurements in mm, wing areas in cm^2 , wingloading in g/cm^2 , weight in g. Exact dimensions recorded following Biggs et al. (1978). Differences between members of mated pairs for any dimension are given as female dimension minus male dimension (positive figures result when females are larger than males, and negative figures when males are larger than females).

Measurement	Males			Females			Mated Pairs		
	n	range	mean \pm S.D.	n	range	mean \pm S.D.	n	range	mean
Bill depth	18	12.5–15.4	14.3 \pm 0.8	18	12.7–16.2	14.4 \pm 0.8	20	-1.1–2.9	0.2
Bill chord	22	20.3–26.2	24.0 \pm 1.3	22	20.2–27.1	24.6 \pm 1.7	26	-4.2–4.6	0.9
Skull length	18	50–55	53 \pm 1.3	17	52–58	54 \pm 1.5	19	-11–5	-0.7
Jaw length	22	37–50	40 \pm 3.8	22	38–48	41 \pm 2.9	26	-10–9	0.5
Jaw-bill length	22	25–36	29 \pm 2.8	22	27–34	29 \pm 1.8	26	-9–6	-0.4
Gape length	21	20–23	22 \pm 0.7	26	20–29	22 \pm 1.7	27	-2–6	-0.3
Tooth depth	22	4.0–5.8	5.0 \pm 0.5	20	3.8–5.7	4.9 \pm 0.6	24	-1.4–1.3	-0.1
Tooth width	22	4.0–5.6	4.8 \pm 0.4	19	4.2–5.7	5.1 \pm 0.4	21	-0.4–1.2	-0.2
Bill depth	23	12.0–18.4	13.8 \pm 1.2	24	12.7–14.8	13.8 \pm 0.5	27	-4.8–1.8	-0.2
Gape width	23	20–25	23 \pm 1.5	26	20–29	23 \pm 1.9	31	-4–6	0.3
Skull width	23	33–37	35 \pm 0.8	26	34–37	35 \pm 0.7	31	-2–3	0.3
Eye spacing	22	26–33	29 \pm 1.3	23	27–30	29 \pm 1.0	27	-4–2	-0.2
Eye diameter	23	7.0–9.6	8.8 \pm 0.6	25	8.0–10.7	9.1 \pm 0.7	27	-1.4–1.7	0.2
Wing length	23	259–298	276 \pm 9.7	27	263–304	285 \pm 10.4	32	-20–41	32
Secondary length	23	130–150	136 \pm 5.2	27	132–150	143 \pm 6.0	30	-4–20	8

Alula length	21	82-96	88±4.5	22	84-100	91±4.7	23	-10-13	4
Ulna length	23	77-86	80±2.6	26	77-87	83±2.4	31	-4-9	3
Humerus length	20	55-81	71±6.3	20	60-78	72±5.0	22	-12-19	3
Femur length	20	45-60	52±4.2	20	47-59	53±3.1	18	-4-6	2
Tibiotarsus length	19	66-77	72±3.7	20	65-80	73±3.8	22	-12-9	1
Tarso-metatarsus length	23	45-54	50±2.6	26	44-61	50±3.2	31	-10-8	0
Toe lengths:									
Inner	23	17-23	19±1.7	26	15-24	20±2.0	30	-5-6	1
Centre	23	26-32	29±1.8	26	25-32	29±1.7	30	-6-5	1
Outer	23	18-23	20±1.6	26	17-23	20±1.7	30	-4-4	0
hind	23	12-19	15±1.6	26	13-18	15±1.3	30	-6-4	0
Claw lengths:									
Inner	23	9.5-14.6	13.0±1.1	25	11.4-15.9	12.8±0.9	29	-2.1-3.5	-0.3
Centre	23	9.4-13.7	12.2±0.8	25	10.6-13.1	11.8±0.7	29	-1.7-1.6	-0.3
Outer	23	5.4-13.7	10.7±1.5	25	9.3-11.7	10.5±0.6	29	-4.4-4.1	-0.1
Hind	23	9.0-14.4	13.3±1.1	25	11.7-18.9	13.5±1.3	29	-1.8-5.4	0.4
Tail lengths:									
Centre	22	140-184	159±9.0	26	148-177	163±7.0	29	-22-22	6
Outer	20	131-166	147±9.0	22	134-163	148±8.0	21	-15-25	3
Primary area	20	178-272	225±24.3	23	181-295	241±31.7	24	-70-78	17
Secondary area	20	137-208	161±19.3	23	127-205	168±18.4	24	-81-38	3
Total wing area	20	348-449	386±28.7	23	337-500	408±43.3	24	-66-100	21
Wing loading	20	.269-.382	.330±0.03	23	.248-.407	.320±0.04	24	-.08-.10	.008
Weight	23	221-299	252±20.0	28	240-312	265±18.0	32	-27-58	17

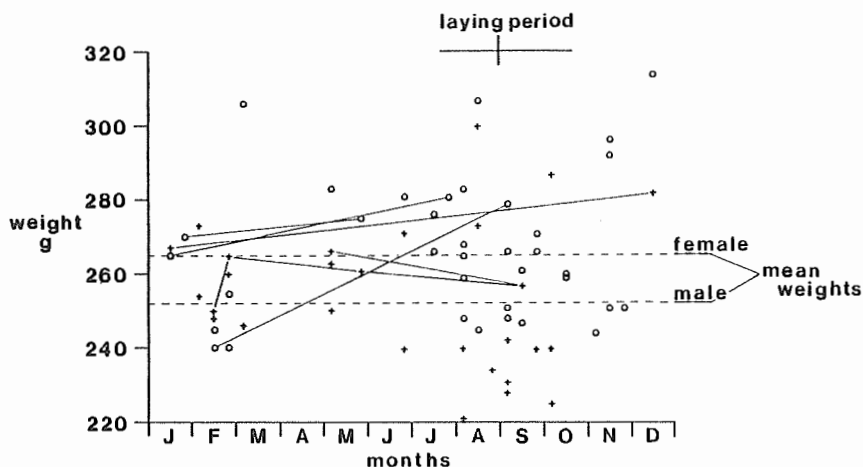


Figure 1: Weight of male (+) and female (0) Greater Kestrels plotted against that third of the month (10–11 days) in which they were captured. Lines connect weights of the same individuals recaptured at different times of the year. The laying period is shown as a mean with the range on either side.

Weight measurements. – The mean weight of males was 252 g and females, 265 g (Table 1). Like linear measurements however, the direction of sexual dimorphism was not constant within pairs, so that males were heavier than females in some pairs. The seasonal distribution of when birds were caught and their weights are shown in Fig. 1. This suggests that inconsistency in the direction of sexual dimorphism may be partly due to seasonal fluctuations in individual weight.

DISCUSSION

Reversed sexual size dimorphism typical of most raptorial birds is evident, on average, for Greater Kestrels. However, when dimensions are compared between members of mated pairs, the extent and direction of dimorphism is not as consistent as might be expected. Such overlap between mates is most likely to occur in a species where sexual dimorphism is slight, such as the Greater Kestrel. American Kestrels (*F. sparverius*) randomly paired without regard to body weight breed successfully in captivity (Bird 1982). In highly dimorphic species there may be little or no overlap between members of pairs. Comparison of reproductive and feeding success of conspecific pairs with differing degrees of dimorphism would go far toward resolving hypotheses about how reversed dimorphism evolved.

Overlap between sexes of the Greater Kestrel, and variability in sexual dimorphism between pairs, may be partly an effect of measurement errors. This could be checked by repeating measurements at the time of capture or recapture, although this was not attempted here. Despite these reservations, and because measurements were all taken by the author and errors are assumed to be consistent, the contention of some overlap between sexes is considered valid.

On average, male Greater Kestrels are larger than females in tooth depth and anterior claw lengths (Table 1). These dimensions may be important in capture of the invertebrate and small vertebrate prey on which both sexes feed. Greater Kestrels ex-

hibit typical falconiform division of labor where a male feeds both the breeding female and young chicks (Kemp 1978). Male Greater Kestrels also have a higher wing loading, especially of the primaries, than females. In the field, it is only possible to sex Greater Kestrels with any confidence when they are in flight. The faster wingbeat and greater speed of the male, derived from its wing proportions, may also be suited to its primary hunting role during the breeding cycle.

The mean weight of 333 unsexed southern African Greater Kestrels has been recorded as 261 g (range 181-334 g) (Biggs et al. 1979). This is very close to the mean of 259 g recorded in this study. Problems of comparison of individual weights result from possible seasonal variations. Figure 1 suggests a tendency for males and females to lose weight in the course of breeding. This might differ from Eurasian Kestrels (*F. tinnunculus*) (Village 1983), where males appear to lose weight when feeding nestlings, while females gain weight prior to laying and retain it during incubation. It would be necessary to know the exact stage of its annual cycle at which each Greater Kestrel was weighed to clarify the pattern of seasonal variation.

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COMPETITION BETWEEN STARLINGS AND KESTRELS FOR NEST BOXES: A REVIEW

THOMAS J. WILMERS

Abstract: A literature search was made on Starling (*Sturnus vulgaris*) use of American Kestrel (*Falco sparverius*) nest boxes, interactions between these species, and nest site selection by Starlings. Extensive Starling use of kestrel boxes has been reported in 4 studies, suggesting a recurring and widespread problem. For nest box programs Starlings appear to shun nest boxes with large entrances and high interior light levels. The possibility that kestrels may have a greater tolerance of these factors than Starlings is discussed.

The American Kestrel (*Falco sparverius*) normally nests in old woodpecker holes and natural cavities in trees (Roest 1957, Smith et al. 1972), but has been found nesting in a variety of other natural sites and man-made structures (Bent 1938, Smith and Murphy 1973, Cruz 1976, Scott et al. 1977, Craig and Trost 1979, Sutton and Tyler 1979). In experiments with captive kestrels, Willoughby and Cade (1964) found that in the absence of a suitable nest cavity, males did not exhibit normal courtship behavior and females failed to ovulate. To offset a presumed shortage of natural cavities, erecting nest boxes for this species has been advocated for many years (see Kalmbach and McAtee 1930). Moreover, Hamerstrom et al. (1973) reported that a kestrel population in central Wisconsin increased substantially when nest boxes were provided in an area with a paucity of suitable nest sites. Since this finding, nest box programs for kestrels have been initiated across North America (i.e., McArthur 1977, Craig and Trost 1979, Stahlecker 1979, Jones 1982, Wilmers 1982, Bloom and Hawks 1983).

One recurring problem meriting attention is the widespread use of kestrel boxes by Starlings (*Sturnus vulgaris*). The purpose of this paper is to review the literature to assess the extent of this problem, discuss interactions between these species, and examine studies of nest box selection by Starlings.

Starlings used 65 of 85 (76%) kestrel boxes in New York (Lincer 1972), 11 of 27 (41%) kestrel boxes in Idaho (Craig and Trost 1979), and 49 of 151 (32%) kestrel boxes in West Virginia and Pennsylvania (Wilmers 1982). In Colorado, boxes erected for kestrels on farmland were used only by Starlings (Stahlecker 1979). Sometimes kestrel nest box programs are discontinued by individuals discouraged by extensive Starling use of boxes (R. Jones pers. comm.).

Competition between these species is poorly understood and remains a conjectural topic pending further research. Cade (1982) suggested that kestrels may not always be able to outcompete Starlings for nest cavities. In one instance a kestrel was driven from a nest cavity by a Starling (Pearson 1936: 239). Kestrels may have abandoned a nest box in Wisconsin when Starlings moved in before the kestrel eggs hatched (Hamerstrom et al. 1973). In West Virginia, Starling nests were found in 4 boxes a short time after kestrels had deserted clutches, but the cause of nest desertion was unknown (Wilmers 1982). Kestrels will sometimes nest in boxes following human-caused destruction of Starling nests (Byers 1980), suggesting that Starling occupancy of a box precludes its use by the falcons. Finally, Starlings will usurp cavities and puncture eggs of birds as large as Wood Ducks (*Aix sponsa*) (Bellrose et al. 1964, Muncy and Burbank 1975), and might well do so at kestrel nests.

From 7 observations, Balgooyen (1976) suggested that kestrels in his California study area outcompeted Starlings for nest cavities, but he did not mention the stage of the kestrels' nesting cycle at the time of these encounters. Kestrels do prey on Starlings (Croft 1958, Smith et al. 1972, Smith and Murphy 1973, Young and Blomme 1975, Wilmers 1982), but nests containing the eggs of both species have been found in Idaho (Craig and Trost 1979), West Virginia (Wilmers 1982), and Washington (A. Pfister pers. comm.). In 2 instances, 2 or more pairs of Starlings and a pair of kestrels nested simultaneously in the same nest tree (Kohler 1915, Doolittle 1926).

Checking kestrel nest boxes weekly to remove Starling nests (Byers 1980) is a time-consuming task and a somewhat ineffective control measure. Starlings can build a nest in 1 day (Kessel 1957: 268). The female will lay and incubate her remaining eggs if a partial clutch has been removed (Kessel 1957: 283), and will start a second clutch 6-9 days after the loss of an incubated clutch (Royall 1966). During 1 breeding season in North Carolina, 56 Starlings which were presumably searching for a nesting site were killed in 1 nest-box trap at 1 site (Stewart 1973).

The development of a nest box that kestrels readily accept, but that Starlings shun, is obviously warranted. In Wood Duck management, apparently no single type of nest box is suitable for all regions (Bellrose 1978), and horizontal metal cylinders to deter Starlings (McGillvrey and Uhler 1971, Heusmann et al. 1977) have been used in some areas. Moreover, Starling boxes have been attached to Wood Duck boxes to reduce competition for nesting sites between these species (Grabill 1977).

Circumstantial evidence for kestrels and studies of Starling nest box selection suggest that kestrels would accept more readily nestboxes with more interior light and/or larger entrances than Starlings. The interior color and size dimensions, as well as the size, positioning and azimuth of its entrance affect light levels within it. In a study of cavity-nesting ducks in Ontario, Lumsden (1976) erected sets of boxes with 3 entrance hole sizes, each box mounted 45 cm apart, and in 102 sets spaced 0.6-1.2 km apart. Of 42 sets used by Starlings, 35 had the smallest entrance (7.5 x 6 cm), 7 the medium (10.5 x 8 cm), and none the largest (13 x 10 cm). Interestingly, the most preferred entrance hole was very similar in size to the 7.6 cm diameter hole used in standard kestrel nest boxes. In a separate experiment with 132 pairs of boxes, one with a black interior and the other unpainted, Starlings chose significantly more boxes painted black inside (Lumsden 1976).

In New Zealand, Moed and Dawson (1979) tested 10 kinds of nest boxes for Starlings, observed that the larger of 2 entrance holes (4.5 cm diameter, 4.5 cm square) was little used, and suggested that Starlings preferred a box providing a dark nest bowl and an entrance providing minimal access clearance.

In Pied Flycatchers (*Muscicapa hypoleuca*), for example, boxes with clean interiors had higher reflected light levels and were used more frequently than boxes with dirty interiors. From this, such factors as a cavity's depth and the size of its entrances were deemed to be of secondary importance, influencing selection of a cavity only to the extent that they affect light (Blagosklonov cited in Lumsden et al. 1980). Based on this inference, Lumsden et al. (1980) suggested that "... it would appear that some species prefer a higher reflected light level, while others, such as the Starling, desire a darker cavity."

In contrast to the above studies, McGillvrey and Uhler (1971) found that adding a series of 7.6 x 10.2 cm holes around the entrances of standard Wood Duck boxes did not prevent Starlings from using the boxes. From this, and because horizontal cylinders with a large entrance (10 x 28 cm) did deter Starlings, they suggested that the size of the entrance might be more important than the amount of light.

Unlike the pale eggs of most cavity-nesting birds, including the pale blue eggs of Starlings (Welty 1975), kestrel eggs are heavily marked (Bent 1938). Hence, the latter's use of cavities may be a relatively recent evolutionary occurrence and perhaps the American Kestrel once used open nests of some type (Richards 1970). Kestrels sometimes nest in snags with open tops (Craig and Trost 1979), and in 1 instance, used a nest box lacking a roof (T. Wilmers pers. obs.). A Starling-deterrent cylinder (McGillvrey and Uhler 1971) was used by a nesting pair of kestrels in Massachusetts (Heusmann et al. 1977). In view of these observations, interior illumination does not appear to be crucial factor in kestrel nest site selection. Eurasian kestrels (*F. tinnunculus*), for example, readily used a nest box with a very large rectangular entrance (Cavé 1968), considerably brightening the box's interior. To my knowledge, this type of box has yet to be tried for the American Kestrel. A controlled experiment comparing kestrel and Starling tolerances for boxes with various entrance sizes and reflected light levels should prove fruitful to kestrel nest box management programs.

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NEST SITE CHARACTERISTICS OF BOXES OCCUPIED BY STARLINGS AND KESTRELS

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Abstract: Recent literature suggests that Starlings (*Sturnus vulgaris*) prefer nest boxes with dark interiors whereas American Kestrels (*Falco sparverius*) prefer brighter ones. We measured the amount of incidental light by photometer in both kestrel- and Starling-occupied nest boxes. Azimuth of, and visibility from, the cavity were recorded to determine their influence on the amount of light in the boxes.

The incidental light in kestrel-occupied boxes was higher ($p < 0.001$). Neither overall visibility from the cavity nor azimuth of entrance differed ($p > 0.05$) between Starling and kestrel nests, but Starling nests with high visibility indices tended to face away from the sun. Kestrel nest box programs can manage against Starling occupation by decreasing the amount of cover above the boxes and by orienting the opening of nest boxes so as to maximize light intensity in them.

Lumsden (1976) conducted tests in Ontario with nest boxes having either black or unstained interiors to conclude that Starlings (*Sturnus vulgaris*) preferred nesting in cavities with darkened interiors. Based on this, Wilmers (1987) proposed that the nest boxes for American Kestrels (*Falco sparverius*) be designed to maximize reflected light levels to deter Starling use. As an easier alternative, we elected to examine factors influencing light levels in an existing nest box design to determine whether these could be manipulated to optimize light levels. Specifically, we hypothesized that by manipulating certain factors (i.e., the orientation of the box to the sun, the amount of foliage surrounding the box), light levels can be maximized to reduce Starling use of kestrel nest boxes. We also tested if Starlings actually occupy nest boxes with darker interiors than boxes used by kestrels.

METHODS

A nest box program for American Kestrels was established by the Macdonald Raptor Research Centre in 1980 on the West Island of Montreal in fallow agricultural land interspersed with natural hedgerows. In most cases, kestrels and Starlings consistently used certain boxes from year to year. However, in several instances Starlings occupied boxes previously used by kestrels.

We compared 8 kestrel and 11 Starling nest boxes from July to August 1984. All nest boxes had internal dimensions of $30 \times 30 \times 40$ cm (L×W×H) with a 7.6 cm entrance hole 7.6 cm from the top of the nest box. Placed in both live trees and dead snags, most boxes were oriented towards the southeast to obtain maximum exposure to the sun and minimize exposure to prevailing weather patterns, but some variation in orientation existed.

Heights of nest tree and nest box were determined using a Ranging 120 range finder. Diameter at breast height (Dbh) of the nest tree was determined using a Lufkin Dbh tape.

The light level in each nest box was likely influenced by the orientation of the box and the amount of foliage surrounding it. Orientation was determined from a compass

reading taken at the nest cavity. The amount of foliage surrounding the box was estimated using an index of the visibility above, below, right and left of the box. A 30 cm \times 3.8 m visibility board divided into 5 equal sections with nine 5.0 cm dots evenly distributed throughout each section was positioned with the center section covering the nest box hole. The board was held in both vertical and horizontal positions. Visibility was estimated by counting the total number of unobstructed dots visible to an observer positioned 30 m from the front of the nest box. The center section was estimated by totalling the number of unobstructed dots seen both horizontally and vertically.

Finally, to determine whether Starlings preferred boxes with darker interiors than kestrels, we used a photometer to measure the amount of reflected light in the box. A photoelectric cell was placed in the center of the box and the door closed. All light measurements were taken on sunny days between 1100 and 1300 hours when the sun was highest in the sky. Readings were on a scale of 1 to 10 microamperes.

Comparisons between groups were performed using both the Mann Whitney U test for univariate data and the Spearman rank correlation test (Siegel 1956).

RESULTS

We found no significant differences in nest tree height, nest box height, and nest tree Dbh between active kestrel- and Starling-occupied boxes (Table 1). All but 1 active kestrel box faced southeast, but only 6 of 11 Starling boxes faced toward this direction (Fig. 1). Mean azimuth between the 2 groups of boxes however, was not statistically different ($p > 0.05$).

Reflected light levels in kestrel boxes were significantly greater than in Starling boxes (Table 2). A high degree of visibility above the nest was positively correlated with high reflected light levels ($r_s = .721$, $p < 0.001$) (Fig. 2).

Table 1: Nest site characteristics of 8 kestrel and 11 Starling active nest boxes in Montreal. No differences ($p > 0.05$).

Characteristic	Kestrel nests (mean)	Starling nests (mean)
Nest tree height (m)	14.9	15.4
Nest box height (m)	5.2	4.9
Nest tree Dbh (m)	47.5	51.5

DISCUSSION

Our results support Lumsden's (1976) findings. Since kestrels commonly nest in dark natural cavities, our finding of higher light levels in active kestrel nests appears to reflect the Starling's preference for dark cavities rather than the kestrel's preference for bright ones. Starlings may compete more aggressively to occupy nest boxes with dark interiors.

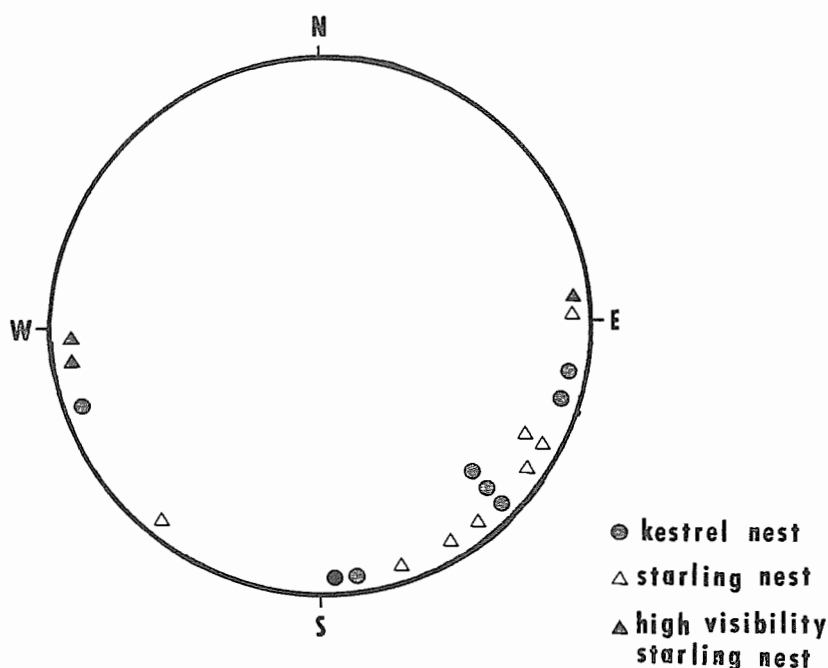


Figure 1: Orientation of kestrel- and Starling-occupied boxes in Montreal.

Table 2: Light-influencing factors at 8 kestrel and 11 Starling active nest boxes in Montreal.

Characteristic	Kestrel nests	Starling nests
Visibility (mean no. of dots)		
Total	73.0	47.5
Above ^a	25.5	13.5
Below	21.1	13.4
Left	20.1	15.0
Right	23.0	14.4
Reflected light levels ^a (mean no. of microamperes)	6.75	2.60

^a – significantly different at 0.05 level.

Balگوoyen (1976) suggested placing kestrel nest boxes in a southeasterly direction so that entrances face away from inclement weather patterns. In Montreal, a southeastern orientation also maximizes the time that the box entrance faces the sun. Though most of the boxes in the study area face the southeast, 6 of the boxes faced other directions. Starlings occupied 5 of them.

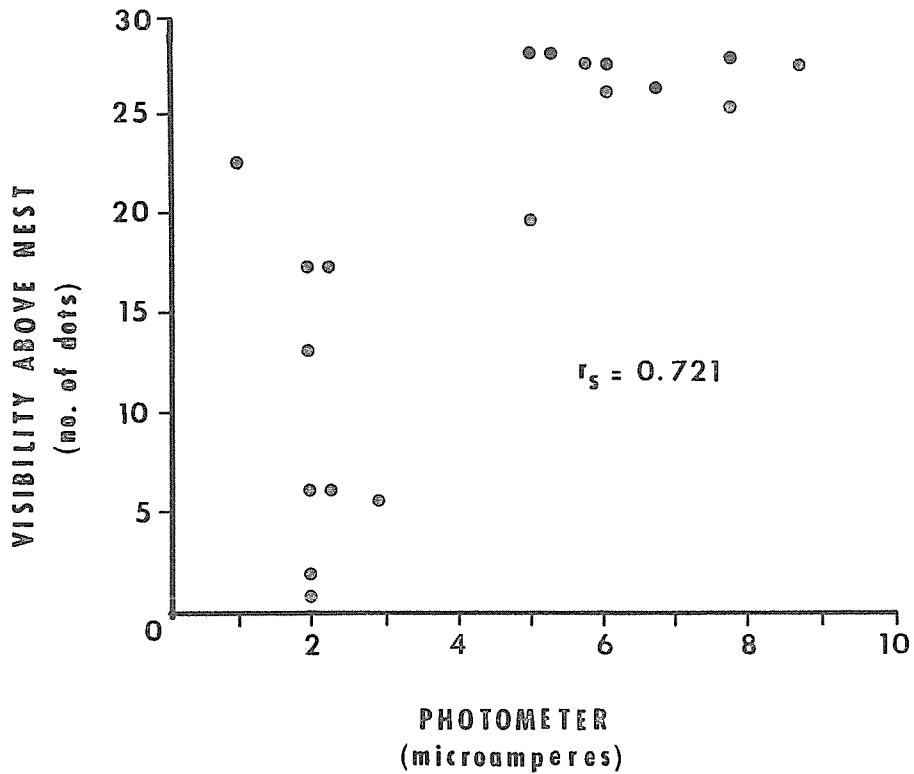


Figure 2: Relationship of reflected light levels in nest boxes with the amount of visibility above them.

Starlings tended to occupy nest boxes with more foliage in front and above the box entrance. However, in 3 instances, they occupied boxes with high visibility above the box, yet low light levels within. Two boxes had westerly orientations and the third faced northeast. Though orientation toward the sun and foliage above the box may influence light levels within the box, we suggest that Starlings do not cue in on these factors; rather, they simply prefer dark boxes regardless of the factors responsible.

Wilmers (1987) suggested that light within the cavity is affected by the azimuth, size and positioning of the entrance, internal dimensions, and color of the cavity walls. Since most of these factors were constant among all our boxes, it would appear that orientation toward the sun and the amount of foliage above the box do influence the amount of light within them.

In other regions, unlike Montreal, orientation of box entrances away from inclement weather patterns may not coincide with maximal light in the boxes, resulting in sheltered yet dark boxes. In areas of dense Starling populations, some consideration for light should be taken.

Wilmers' (1986) suggestion for a new nest box design has merit for future nest box programs, but the problem for existing nest box programs may be dealt with more easily

by manipulating the orientation and surrounding cover of nest boxes to maximize light levels, thus possibly deterring Starlings from aggressively competing for them.

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THE USE OF KESTRELS IN TOXICOLOGY

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Abstract: Various species of kestrels have become important bioindicators of environmental quality and test species for comparative toxicology in captivity. At least 7 species of kestrels have been used to document the presence of environmental contamination, primarily organochlorines and metals, in at least 15 countries. Captive kestrels have been used in studies involving a wide variety of environmental contaminants and toxicants examining: bioaccumulation; lethal toxicity using acute, chronic, and secondary exposures; effects on reproduction, eggshell thickness, and related enzyme systems; and effects on a wide variety of physiological and biochemical parameters. Field studies have examined the response of kestrels to exposure to insecticides. Kestrels should continue to play a vital role as a bioindicator and raptorial "white mouse", especially because of their relationship to other falconiformes, several of which have been shown to be extremely sensitive to environmental changes.

Toxicology has been defined as "a science that deals with poisons and their effect on living organisms, with substances otherwise harmless that prove toxic under particular conditions, and with the clinical, industrial, legal or other problems involved" (Gove 1965). In spite of Webster's definition, we will make a couple of minor excursions.

The first excursion deals with the quintessential role that basic research played and still plays. Some of us who have happened to be working on topics that were in vogue (such as eggshell thinning in birds of prey), do not want to forget that we are standing on the shoulders of others before us. Without the work of Willoughby and Cade (1964), we would not have known that the American Kestrel (*Falco sparverius*) could be bred in captivity in numbers that would support extensive colonies for toxicological purposes. Little did these early researchers know that their efforts to provide "...a convenient starting point for comparative studies of falconiform behavior" would result in widespread use of the captive and captive-bred kestrel for comparative toxicology. While Willoughby and Cade (1964) were breeding American Kestrels in captivity, similar work was being conducted on this species in Germany, followed by limited work with Eurasian Kestrels (*F. tinnunculus*) (Koehler 1968). These early studies were followed by the establishment in 1964 of a large captive colony of breeding American Kestrels by W.H. Stickel and F.C. Schmid at the Patuxent Wildlife Research Center, Laurel, Maryland, (Porter and Wiemeyer 1970, 1972b) which was used for toxicological studies. These pioneering efforts resulted in the widespread use of captive and captive-bred kestrels for comparative toxicology and other areas of research, not only in the United States, but also in Canada (Bird 1982, 1985) and Europe, as we will describe later. By 1979, a small colony of Eurasian Kestrels was also established at the University of Bristol, Great Britain (Kirkwood 1980).

The kestrel has become the "white mouse" of the raptor world for at least two reasons: (1) basic research, showing that it was easily bred in captivity, had been done at a timely point in history, and (2) being common and cogenetic with the Peregrine Falcon (*F. peregrinus*), this important taxonomic relationship resulted in our perception of the kestrel as a bioindicator of not only our environmental quality but, under controlled conditions, of what was happening to other falconiform species.

In preparing this review, several computer databases and our personal files were searched for pertinent references. The literature cited section of each acquired reference

was scanned for additional references pertaining to the subject. In addition, several scientists and institutions known for their kestrel toxicology work were contacted to identify and include any ongoing or recent and not-as-yet published data. The great preponderance of literature cited is in English. We expect that we have, unintentionally, omitted many references in other languages and hence, welcome copies of such papers.

PRESENCE AND TRENDS OF CONTAMINANTS IN WILD POPULATIONS

Presence. - The American Kestrel has documented the presence of environmental contaminants in at least 6 states and Canada, the Eurasian Kestrel in 9 countries, and the Grey Kestrel (*F. ardosiacus*), Lesser Kestrel (*F. naumanni*), Greater Kestrel (*F. rupicoloides*), Australian Kestrel (*F. cenchroides*), and Mauritius Kestrel (*F. punctatus*) in 1 country each (Table 1).

Chemicals found in these bioindicators of environmental quality have run the gamut from BHC and chlordanes, through the "alphabet soup" of DDT-derived acronyms, dieldrin, endrin, heptachlor epoxide, and other organochlorine biocides, to the industrial polychlorinated biphenyl (PCB), polychlorinated naphthalene (PCN), polychlorinated terphenyl (PCT) series, the fungicide HCB, the heavy metals mercury, copper, lead, and cadmium, the organophosphates mevinphos and parathion, the oral anesthetic alphachloralose, fluoride, and various radionuclides (Table 1).

Trends. - Fuchs et al. (1972) presented an interesting picture of several organochlorines (including PCB's and HCB) in birds of prey of Netherlands over the period 1965-71. The Eurasian Kestrel reflected a trend *opposite* to all other raptor species with respect to DDE and PCB's (i.e., not an obvious decrease) for that time period; however, sample sizes were small. Cooke et al. (1982) presented trend data for DDE, dieldrin, and PCB's in livers of Eurasian Kestrels in Great Britain for the years 1963-77. Dieldrin concentrations were similar for the years 1963-75, followed by a significant decline in 1977. DDE concentrations in the early 1970's were similar to those in the mid-1960's, with an intermediate peak in 1969, followed by gradual decreases thereafter. PCB concentrations were significantly lower for the period 1972-75 than 1967-71; concentrations in 1977 were similar to those in 1972-75.

EFFECTS OF CONTAMINANTS ON CAPTIVE KESTRELS

Bioaccumulation under controlled conditions. - Many authors have reported on the bioaccumulation and pharmacodynamics of organochlorines (Bernard 1962, Prestt et al. 1968, Wiemeyer and Porter 1970, Porter and Wiemeyer 1972a, Vos et al. 1972, Lincer 1972, 1975, Stickel et al. 1979, Henny and Meeker 1981, Rudolph et al. 1983, 1984, Wiemeyer et al. 1986b). Serafin (1984) reported on the intestinal absorption of dieldrin, PCB, and mercury. The accumulation of lead in tissues has also been reported by several authors (Stendell 1980, Franson et al. 1983, Pattee 1984, Custer et al. 1984, Hoffman et al. 1985b). Koeman et al. (1971) reported on mercury residues in tissues of Eurasian Kestrels dosed with methylmercury. Bird and Massari (1983) and Carriere et al. (1987) reported on the uptake of fluoride residues in bones of American Kestrels dosed with sodium fluoride or fed cockerels raised on a diet containing fluoride, respectively.

Lethal toxicity. - The acute toxicity (that resulting from a single dose) to American Kestrels of a number of chemicals has been reported. These include the organophosphates parathion (Rattner and Franson 1984) and fenthion (Schafer et al. 1969); the bird control agents DRC-1339 (DeCino et al. 1966), DRC-1347 (Schafer et al. 1969), and 4-aminopyridine (Avitrol) (Schafer et al. 1973), the organochlorine insecticide endrin (Schafer et al. 1969), and sodium cyanide (Wiemeyer et al. 1986a). The toxicity

of many of these toxicants was also summarized by Schafer (1972) and Schafer et al. (1983).

The potential hazard of secondary poisoning to American Kestrels of a number of these toxicants including Avitrol (Holler and Schafer 1982), DRC-1339 (DeCino et al. 1966), DRC-1347 and fenthion (Schafer et al. 1969), and parathion (Fleming et al. 1982), in addition to the anticoagulant chlorophacinone (Radvanyi 1983), has also received attention.

Chronic doses (given in the diet over a period of time) of a variety of organochlorine contaminants have resulted in deaths of captive kestrels in a number of studies. Bernard (1962) fed sparrows which had been dosed with 300 ppm DDT to American Kestrels which, in turn, died of DDE poisoning. Prestt et al. (1968) provided data on dieldrin residues in livers of Eurasian Kestrels that had been dosed with dieldrin. HCB dosage (200 ppm) of Eurasian Kestrels resulted in the death of one bird after 62 days (Vos et al. 1972). A number of American Kestrels given long term dietary dosages of DDT plus dieldrin (4.2 ppm DDT and 0.84 ppm dieldrin or 1.4 ppm DDT and 0.28 ppm dieldrin) or DDE (2.8 ppm) alone died of dieldrin or DDE poisoning, respectively (Porter and Wiemeyer 1972a, Wiemeyer et al. 1986b). Henny and Meeker (1981) reported that several American Kestrels given chronic doses of DDE (160 or 250 ppm) died of DDE poisoning. Chronic exposure by contaminants, other than organochlorines, also has resulted in deaths of American Kestrels. Sodium fluoride at 500 ppm in the diet of American Kestrels resulted in mortality (Bird and Massari 1983). One of 8 American Kestrels died following exposure to a chronic dose of 3% crude oil in the diet (Pattee and Franson 1982). Mortality of nestling American Kestrels, given daily doses of lead (Hoffman et al. 1985b) and paraquat (Hoffman et al. 1985a), has been reported.

Sublethal effects. - Effects of the sublethal level, often brought about by long-term (i.e., chronic) exposure to biologically active chemicals have historically been shown to be extremely important, one notable example being eggshell thinning. Many papers have addressed the topic of eggshell thinning in kestrels, most notably the work done at the Patuxent Wildlife Research Center and Cornell University.

In particular, Wiemeyer and Porter (1970) reported that, under controlled conditions, 2.8 ppm DDE diet over 1 year resulted in a 10% decrease in eggshell thickness. Lincer (1975) showed a dose-response relationship between DDE and eggshell thinning in a captive kestrel population and revealed that the correlative DDE-eggshell thinning relationship was not statistically different for captive experimental birds and a local wild population.

Lincer (1972) illustrated the impact of dietary DDE on carbonic anhydrase in the American Kestrel and Peakall et al. (1973) reported that a 3 ppm DDE diet actually resulted in a lowered rate of water loss through eggshell than controls, despite significant eggshell thinning. They also showed, through scanning electron microscopy, that dietary DDE resulted in fewer, but larger, pores in the eggshell than in controls. Additional eggshell structural changes, as the result of DDE dosage of kestrels, were also reported by Kiff et al. (1979).

Khan and Cutkomp (1982) showed the differential sensitivity of Mg^{2+} ATPase in the shell gland and other tissues to DDE and the differential sensitivity of 3 avian species, including the American Kestrel. In looking for an enzymatic basis for cause-and-effect, they found that the sensitivity of ATPase to DDT in the kestrel shell gland was not obviously different from that in the kestrel brain, unlike the response of DDE. Bird et al. (1983a) reported that dietary DDE and the resulting 26% eggshell thinning was accompanied by significantly reduced activity of Ca-ATPase and carbonic anhydrase, but no effect on circulating calcium levels.

Table 1: Reports of environmental contaminants in wild kestrels.

Species and collection area	Collection year(s)	Sample type ^a	Contaminants reported ^b	Source
American Kestrel (<i>Falco sparverius</i>)				
California	1963-65	E	OC	Keith and Hunt (1966)
	1967-68	WB,E	OC,PCB	Risebrough et al. (1968)
	1978	E	OC,PCB	Rudolph et al. (1983)
Florida	1971-73	F,U	OC	Johnston (1976)
	1973-76	F,U,B	OC	Johnston (1978)
Idaho	1976	WB	RN	Craig et al. (1979)
Idaho-Oregon	1974-76	BP,E	OC,PCB	Henny (1977)
	1974-76	BP,E	OC,PCB	Henny and Meeker (1981)
Oregon	1978-81	E,B	OC,PCB	Henny et al. (1983)
New York	1969-72	E	OC,PCB	Lincer (1972, 1975)
	1970	E	Hg,Cu,Cd,Pb	Lincer and McDuffie (1974)
	1970-72	E	OC,PCB	Lincer and Clark (1978)
	1971-72	Prey	OC	Lincer and Sherburne (1974)
	1979	SC	Parathion	Stone et al. (1984)
	1980	B	OC,PCB	Stone (1981)
Washington	1981-82	B,E	OC	Blus et al. (1983)
Canada	1968-69	L	Hg	Fimreite et al. (1970)
	-	E	OC	Keith and Gruchy (1972)
Eurasian Kestrel (<i>Falco tinnunculus</i>)				
Belgium	1969	E	OC	Joiris and Martens (1971)
	1971	E	OC	Joiris and Martens (1973)
Denmark	-	L	OC,PCB	Karlog et al. (1971)
	1874-1974	ES,E	OC,PCB,Pb	Grandjean (1976)
Germany	1974-76	E	OC	Conrad (1977)
Great Britain	1961	IO	OC,Hg	Cramp et al. (1962)
	1961-62	M,L	OC,Hg	Cramp (1963)
	1961-62	IO	OC,Hg	Cramp et al. (1963)
	1962-63	B,L,K,M	OC,Hg	Cramp et al. (1964)
	1963	E	OC	Ratcliffe (1965)
	-	L	OC	Harrison (1966)
	1963-64	E,M,L,B	OC	Walker et al. (1967)
	1963-64	IO,L,E	OC,Hg	Cramp and Conder (1965)
	-	L	PCB	Holmes et al. (1967)
	-	E	OC,PCB	Ratcliffe (1970)
	1962-65	L	OC	Davis (1966)
	1963-65	L,E	OC	Prestt (1967)
	to 1965	L,E	OC	Moore (1965)
	-	E	OC	Robinson (1967)
	1962-69	L,E	OC,PCB	Prestt and Ratcliffe (1972)
	1966-68	L,E	OC,PCB	Prestt et al. (1970)
	-	L	PCT,PCB	Hassell and Holmes (1977)
	-	L,M,K	PC,PCB,PCN	Cooke et al. (1980)
	1963-77	L,F,B	OC,PCB,Hg	Cooke et al. (1982)
	1963-79	L	OC	Newton et al. (1982)

Great Britain	1971-76 ^c	-	-	Brown et al. (1977)
	1966-80	L,M	OC,PCB	Keymer et al. (1981)
	1966-80	SC	Mevinphos	Keymer et al. (1981)
	1966-80	-	Alpha-chloralose	Keymer et al. (1981)
	1973-79	-	-	Hamilton et al. (1981)
	1976-82	Bone	Fluoride	Seel and Thomson (1984)
	1979-82	L,K	Pb	Macdonald et al. (1983)
Israel	1949-64 ^d	-	-	Mendelssohn (1972)
	1975-76 ^e	-	-	Mendelssohn and Paz (1977)
Netherlands	1960 ^f	-	-	Bruijns (1963)
	1965	B,L,M	OC	Koeman and van Genderen (1965, 1966)
	1966	L	OC	Fuchs (1967)
	1968-69	B,L,K	OC,PCB,Hg	Koeman et al. (1969)
	1968-71	L	OC,PCB	Fuchs et al. (1972)
	1968-71	L	PCB	Koeman (1973)
Norway	1967	E	Hg	Holt (1969)
	1965-76	L,K,M,B,	OC,PCB,Hg	Holt et al. (1979)
Sweden	1963-64	L,K	Hg	Borg et al. (1969)
Switzerland	1973-77	L,E	OC,PCB,Pb,	Juillard et al. (1978)
				Hg,Cd
Gray Kestrel (<i>Falco ardosiaceus</i>)				
Nigeria	1974-76 ^g	-	-	Koeman et al. (1978)
Lesser Kestrel (<i>Falco naumanni</i>)				
Israel	1949-64 ^h	-	-	Mendelssohn (1972)
Greater Kestrel (<i>Falco rupicoloides</i>)				
South Africa	1975	B,L	OC,PCB	Peakall and Kemp (1976)
Australian Kestrel (<i>Falco cenchroides</i>)				
Australia	1980	F,L,S,I	OC	Saunders and Cooper (1982)
Mauritius Kestrel (<i>Falco punctatus</i>)				
Mauritius	1979-80	L,B	OC	Cooper et al. (1981)

^a E=egg, F=fat, U=uropygial gland, B=brain, WB=whole body, BP=blood plasma, L=liver, M=muscle, K=kidney, SC=stomach contents, S=stomach (proventriculus and ventriculus), I=intestine, ES=eggshell, IO=various internal organs.

^b OC=organochlorine pesticide(s), PCB=polychlorinated biphenyls, RN=radionuclides, Hg=mercury, Cu=copper, Cd=cadmium, Pb=lead, PCT=polychlorinated terphenyls, PCN=polychlorinated naphthalenes.

^c Kestrels listed among other predatory birds as having died of poisoning by several toxicants; details of specific cases not given.

^d Thallium poisoning implied; no analyses reported.

^e Deaths occurred following Azodrin use; no analyses reported.

^f Mortality said to result from parathion; no analyses reported.

^g Possible reduction in numbers following dieldrin use; no analyses reported.

^h Disappearance may have been due to organochlorine poisoning; no analyses reported.

A dietary combination of dieldrin and DDT which mimicked field levels (i.e., 0.28 and 1.4 ppm, respectively) resulted in a 77% decrease in eggshell thickness in a captive population of American Kestrels (Porter and Wiemeyer 1969, Wiemeyer et al. 1986b). Interestingly, the impact was heightened to a 17% decrease in first-generation birds and a 23% decrease in a combined group of first and second generation birds.

Because eggshell-thinning in kestrels has been associated with eggs containing PCB's (Lincer 1972, 1975), many have suggested that a cause and effect relationship might exist. Unfortunately, levels of PCB's are usually also correlated with DDE and other organochlorine biocides. Lincer (1972) tested the combined effects of 3 ppm DDE and 10 ppm PCB's on eggshell thickness of American Kestrels. Dietary PCB's alone did not have any effect on eggshell thinning, but significantly increased the impact of DDE on eggshell thinning. Interestingly, 100% of the pairs on a combination of DDE-PCB diet exhibited egg breakage whereas none of the pairs on either DDE or PCB alone displayed any egg breakage. In addition, there was a suggestion that the combination diet also resulted in a delayed first egg date.

In searching for a biochemical basis for observed raptorial reproductive problems, Lincer and Peakall (1970) exposed kestrels to diets containing 0.5 or 5.0 ppm PCB's. These diets resulted in increased cytoplasmic RNA, and a dose-dependent *in vitro* breakdown of estradiol. They concluded that the physiological actions of PCB's are similar to those of DDT and its metabolites.

Significant induction of hepatic microsomal ethylmorphine N-demethylase activity was obtained in kestrels fed dietary dosages of DDT plus dieldrin or DDE (Gillett et al. 1970). The hydroxylation of biphenyl and coumarin *in vitro* by liver preparations of kestrels and other species was reported by Leeuwangh (1972).

Pattee (1984) clearly demonstrated that dietary levels of 50 ppm metallic lead did not result in any adverse effect on eggshell thickness. Similarly, Peakall and Lincer (1972) found that a dietary load of 10 ppm methylmercury did not result in any change in eggshell thickness of kestrels.

Several investigators have conducted studies on the effects of contaminants on reproduction, somewhat apart from specific effects on eggshell thickness. Porter and Wiemeyer (1969) dosed kestrels with DDT plus dieldrin and found increased egg disappearance, and reductions in the number of eggs that hatched and young that fledged in dosed vs. control groups. The pattern of reproductive failure of the dosed kestrels was remarkably similar to that of declining wild raptor populations. In a later paper (Wiemeyer et al. 1986b) dealing with the same study, contaminant concentrations in the tissues and eggs of the dosed birds were reported. Concentrations of each toxicant (DDE, DDD, DDT, and dieldrin) were usually highly correlated among tissues. Organochlorine concentrations in brains and eggs could be predicted from concentrations in carcasses. Of the 4 toxicants in eggs, DDE was significantly and most closely correlated with fledging success. Henny and Meeker (1981) later provided data on relationships between DDE concentrations in plasma and brain for DDE dosed captive American Kestrels and for plasma and eggs in free-living wild American Kestrels. Cooke et al. (1982) have demonstrated the relationship between residue concentrations of organochlorines in brain and liver of wild Eurasian Kestrels.

Bird et al. (1983b) studied the effects of PCB and mirex exposure on semen characteristics of American Kestrels. Mirex alone produced a decline in sperm concentration with a compensatory increase in semen volume. Aroclor 1254 produced a decline in sperm concentration and temporal patterns in semen characteristics.

Pattee (1984) fed American Kestrels 50 ppm metallic lead in the diet and found no effects on egg laying, initiation of incubation, or fertility.

Bird and Massari (1983) studied the effects of sodium fluoride on reproductive performance, however there were problems with sample sizes and statistical procedures. Carriere et al. (1987) re-analyzed the data and showed that the fluoride treatments had no effect on clutch size, eggshell thickness, percent fertility and hatchability, and fledging success. Even in kestrels fed cockerels with fluoride in their femur, Carriere et al. (1987) detected no effects on clutch size, percent fertility and percent hatchability. In both studies, eggshell fluoride content was very sensitive to fluoride exposure.

Hand-raised kestrels fed 0.0112 g of fluoride per day for 21 days had more than 10,000 ppm of fluoride in their femur without suffering growth depression (D. Carriere and D. Bird, unpubl. data).

Other sublethal toxicological effects have been examined using the kestrel, including prey capturing behavior (Rudolph et al. 1983, 1984), growth and development including physiology and morphology (Rattner and Franson 1984, Hoffman et al. 1985a,b,c), hematology (Vos et al. 1972, Pattee and Franson 1982, Franson et al. 1983, Custer et al. 1984, Hoffman et al. 1985c), histology and cytology (Lincer 1972, Vos et al. 1972, Peakall et al. 1973, Kiff et al. 1979, Franson et al. 1983, Hoffman et al. 1985a), and specific biochemical changes (Gillett et al. 1970, Lincer and Peakall 1970, Leeuwangh 1972, Lincer 1972, Vos et al. 1972, Fleming et al. 1982, Khan and Cutkomp 1982, Pattee and Franson 1982, Bird et al. 1983a, Franson et al. 1983, Rattner and Franson 1984, Rudolph et al. 1984, Hoffman 1985a,c).

FIELD OBSERVATIONS - SUBLETHAL EFFECTS

A number of field studies have reported eggshell thickness in relation to pre-DDT thickness. Ratcliffe (1970) documented normal eggshell thickness (including shell weight and thickness index) for Eurasian Kestrels in Great Britain and its decline after 1947. Similar work was conducted for American Kestrels in North America by Anderson and Hickey (1972). Many of the studies that have reported on contaminants in eggs of wild kestrels (see Table 1) have also provided data on shell thickness. Taking a comparative spatial approach, Henny (1977) reported that eggshells were 10% thinner in an area sprayed with DDT for tussock moth control than in areas 13-28 km from the spray site. Tendencies toward smaller clutches and lower fledging rates in the spray area vs. the non-spray area were noted.

Henny et al. (1983) found reduced productivity of American Kestrels in an area where heptachlor was used on wheat seed for wireworm control. The reduced productivity occurred when heptachlor epoxide exceeded 1.5 ppm in the eggs. Incidentally, the female that laid the egg containing the highest heptachlor epoxide residue (9.1 ppm) during the study was later found dead in the nest box with a lethal concentration of heptachlor epoxide in her brain. Heptachlor epoxide did not thin eggshells.

Lincer and McDuffie (1974) reported that heavy metals in kestrel eggs laid near Ithaca, New York, were relatively low, and found no obvious inverse relationships between eggshell thickness and mercury, copper, or lead. Grandjean (1976) reported a correlation between increased eggshell lead concentration and decreased shell thickness in Eurasian Kestrels; however, he recognized the confounding correlative relationship between lead, PCB's, and other organochlorines. The inverse relationship between shell thickness and eggshell lead was not supported by the work of Pattee (1984) with captive American kestrels.

Wild kestrels living in non-polluted areas had between 502.9 and 781.1 ppm of fluoride in their femur, however fertility did not appear affected (D. Carriere and D. Bird, unpubl. data).

RECOMMENDATIONS FOR FUTURE WORK

In the future, the kestrel will likely continue to play a vital role as a bioindicator and raptorial "white mouse". It has particular applicability to endangered species, being a member of the order Falconiformes. Many falconiforms such as the Peregrine Falcon, Bald Eagle (*Haliaeetus leucocephalus*), and Osprey (*Pandion haliaetus*) have been shown to be extremely sensitive to environmental changes. Kestrels, being non-endangered, small, and readily maintained and bred in captivity, can be used for new approaches in monitoring environmental contamination and can continue to serve as a prototypical test species. Future emphasis on contaminant research involving kestrels will probably involve more detailed studies on metals, rodenticides, organophosphates, and new contaminants. Wild kestrels are readily attracted to nest boxes, thereby facilitating adequate sample sizes in field studies where large samples are required in both "clean" and "contaminated" areas (Henny 1977, Henny et al. 1983). The kestrel, being somewhat more tolerant of disturbance and habitat changes than other falconiforms, and because of its position in food chains, could serve as a valuable species for monitoring contaminants in agricultural areas.

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