Habitat Sampling

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INTRODUCTION

Understanding why animals are not distributed randomly across the landscape has been a main objective of ecology for some time (Cody 1985, Wiens 1989a). Students of the relationships between organisms and their habitats usually assume that individuals select where they choose to live (Cody 1985), and that it is possible to find correlations between the distribution, abundance, and demography of organisms and environmental variables (Buckland and Elston 1993, Morrison et al. 1998, Rushton et al. 2004, Guisan and Thuiller 2005). The search for correlations of this kind is common in studies of "habitat selection" (Anderson and Gutzwiller 1994, Litvaitis et al. 1994, Garshelis 2000, Jones 2001), although less attention has been given to the patterns of behavior that underlie choosing a place to live.

Because managing populations largely depends on managing or maintaining habitat (Anderson and Gutzwiller 1994), habitat use often is a basic element in conservation and management plans (Anderson et al. 1994, Edwards et al. 1996, Norris 2004). The assumption underlying these plans is that species will reproduce or survive better in habitats they prefer. Although it is an integral part of wildlife management, the process of evaluating what constitutes appropriate habitat for a given species or population can be difficult to achieve and often is beset with problems. Many of the problems involved have been recognized, and published discussions of them have prompted a host of evolving sampling designs and methods (Anderson and Gutzwiller 1994, Litvaitis et al. 1994, Garshelis 2000, Jones 2001, Hirzel et al. 2002, Guisan and Thuiller 2005, MacKenzie et al. 2006). In this chapter, we review the scope and objectives of habitat studies in raptors, and the methods for quantifying raptor habitats. We emphasize that studying the habitats of raptors essentially is no different than studying the habitats of any other group of organisms; thus, literature on habitat studies from almost any species is useful when designing a study on raptors.

TERMINOLOGY

Habitat terminology is not well defined. For example, the semantic and empirical distinctions between the terms "habitat use" (i.e., where individuals are) and "habitat selection" (i.e., where they choose to be) often are unclear (Garshelis 2000, Jones 2001). Any discussion of habitat sampling must be based on clearly defined terms. We recommend the following, based on Hall et al. (1997), Morrison et al. (1998) and Kennedy (2003) for studies of raptor habitat.

Habitat: the resources and conditions present in an area that produce occupancy by raptors. This is a synonym for the "niche" of the raptor according to the Grinnellian concept of the niche.

Habitat use: the way in which a raptor uses a collection of physical and biological components (i.e., resources) within a defined area and time.

Habitat abundance: the amount of habitat within a defined area and time.

Habitat availability: the amount of habitat that is exploitable by a raptor within a defined area and time.

Habitat selection: an hierarchical process involving a presumed series of innate or learned responses, or both, made by raptors regarding what habitat to use at different scales of the environment.

Habitat preference: the consequence of a raptor's habitat selection process, resulting in disproportionate use of some areas over others.

Habitat quality: the relative ability of habitats to provide conditions appropriate for raptor survival and reproduction.

Landscape: a mosaic of environmental patches across which raptors move, settle, reproduce and die. In principle, the landscape containing a raptor population can be mapped as a mosaic of suitable and unsuitable patches. Each map must be at a scale appropriate to the raptor under study.

OBJECTIVES

When designing an ecological study, the first step is to develop a clear list of objectives (Starfield 1997). Objectives should provide information about the intent of the study and the level of acceptable uncertainty. Moreover, appropriate objectives, combined with a good introduction, should describe clearly how the study would enhance understanding in ecology or implementation of management actions. The following questions should be among those considered when developing objectives: What question is being asked and how does it advance understanding of ecological processes, or the requirements of the species under investigation? What is the focus of the study? Is it a population, a species (all populations) or a community that is being studied? What temporal and spatial scales are being considered?

Most habitat studies are searches for patterns, and not experimental tests about hypothesized underlying ecological processes. Because of this, objectives usually are expressed in the form of a question, or statistical hypothesis. If an explanation about a process involved in habitat selection is being tested via the hypothetical-deductive method (e.g., field experiments), then a statement indicating that the study involves the test of research hypotheses, as defined by Romesburg (1981), would be an appropriate objective.

CONSIDERATIONS FOR STUDY DESIGN

Excellent overviews of the basic principles of study design can be found in Ford (2000), Quinn and Keough (2002), and Williams et al. (2002). Important elements of design that should be considered at the outset of any habitat study involving a search for patterns include the proposed scope of inference of the study, and random and adequate sampling procedures. Below we describe several conceptual and practical elements that are central to studies of habitat and potentially influence study design.

Temporal and Spatial Scales

Factors that explain ecological processes usually are scale-dependent (Wiens et al. 1987, Mitchell et al. 2001, Sergio et al. 2003). Populations, for example, usually are influenced by how habitat is distributed across the landscape in both space and time (Wiens 1989b, Levin 1992, Corsi et al. 2000, Martínez et al. 2003). Study designs must be consistent with the abilities of the subject species to perceive and move among existing habitat patches, and investigators should consider the various scales at which habitat features may have influence (Litvaitis et al. 1994, Pribil and Picman 1997, Morrison et al. 1998, Rotenberry and Knick 1999, Sánchez-Zapata and Calvo 1999, Mitchell et al. 2001). There are at least three levels of spatial scale used by raptors during the breeding season: the nest area, the post-fledging family area (PFA), and the foraging area (Fig. 1). The nest area (or nest site), which typically is defined as the area immediately around the nest, often contains alternative nests and may be reused in consecutive years. The PFA surrounds the nest area and is defined as the area used by the family group from the time the young fledge until they no longer are dependent on the adults for food. The foraging area is the area used by the provisioning adults and typically encompasses the remainder of the home range during the breeding season. Below we use the Northern Goshawk (*Accipiter gentilis*) to illustrate the relative sizes of these areas and how interpretation of Northern Goshawk habitat can vary depending on the scale used to define nesting habitat.

In North America, nest areas of Northern Goshawks typically are less than 20 ha (DeStefano et al. 2006, Squires and Kennedy 2006,). Mean PFA size ranges from 60 to 170 ha depending on local environmental conditions (Kennedy et al. 1994, McClaren et al. 2005), and home ranges during the breeding season vary between 570 and 5,300 ha, depending on sex, habitat characteristics, and choice of home-range estimator (Squires and Kennedy 2006).

McGrath et al. (2003) evaluated goshawk nesting habitat empirically at various spatial scales to develop models that could be used to assess the effects of forest management on suitability of nesting habitat. Their work compared nesting habitat on four study areas in the inland Pacific Northwest during 1992-1995 and used four stand structures that represent different stages of stand development following disturbance. Eight habitat scales ranging from 1 to 170 ha (PFA scale; they did not analyze foraging habitat) surrounding 82 nests and 95 random sites were analyzed. A few key points are relevant to this chapter: (1) the ability to discriminate goshawk nest sites from available habitat decreased as landscape scale increased; (2) at the 1-ha scale, the stem exclusion stage of stand development (onset of self-thinning, no regeneration and the beginning of crown class differentiation into dominant and subordinate species) was preferred, whereas understory re-initiation (colonization of the forest floor by advanced regeneration and continued overstory competition) and old-growth (irregular senescence of overstory trees and recruitment of understory trees into the overstory) phases were used in proportion to their availability; (3) at larger scales, the middle stages of stand development consisting of stem exclusion and understory re-initiation (both with canopy closure > 50%) were preferred, suggesting that the types of habitats used increased as scale increased.

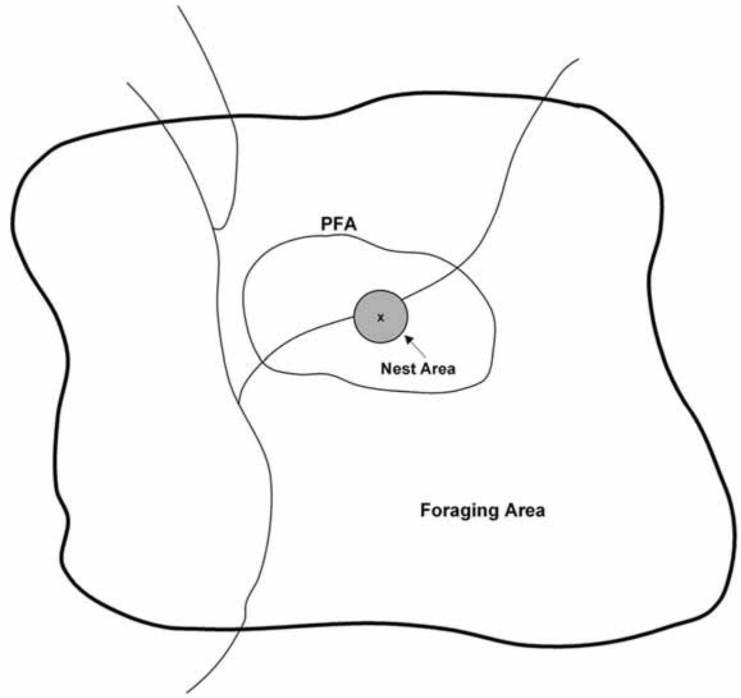

Figure 1. Conceptual diagram of three levels of spatial organization at a raptor nest in a drainage, including nest area, post-fledging area (PFA), and foraging area (from Squires and Kennedy 2006). (See text for definitions of area types.)

The influence of habitat features at different spatial scales is likely to be species-specific, and can change with body size, mobility and life history requirements. Thus, the commonly used terms "macrohabitat" and "microhabitat" are relative; a macrohabitat feature for a relatively wide-ranging, mobile species may be characterized on a much larger geographic scale than a macrohabitat feature for a less mobile species. However, even raptors of limited mobility can move rapidly over large areas. The accuracy with which a raptor can be placed at a particular point and time is an important consideration for habitat assessment at the microscale. For example, determining how a vegetation type is used depends on the accuracy of the bird's location (Withey et al. 2001) and how accurately sites are sampled relative to the size and distribution of patches of vegetation.

Raptors also exhibit temporal variation in habitat preferences. Studies of habitat and subsequent descriptions of a species habitat in management plans should account for these temporal changes. A relatively long-time scale would be an examination of the effects of plant succession and disturbances (measured in years) on the habitat of a raptor. In contrast, a short time-scale is exemplified by studies that measure vegetation in conjunction with momentary behavioral events such as an attempt to catch prey.

Some species use particular habitats during specific periods of the year, and only an assessment of habitat use during a complete annual cycle would describe the species habitat preferences. Northern Goshawks, for example, occupy a much broader range of habitats during the winter than during the nesting season. Because of this, breeding season habitat evaluations do not fully describe Northern Goshawk habitat patterns. A hotly debated management question regarding this species is whether or not it is a specialist that depends upon mature forest habitat. In their recent review of Northern Goshawk ecology, Squires and Kennedy (2006) addressed this question and concluded that the answer depends upon the season and residency patterns of the birds. This species is a partial migrant, meaning that some individuals occupy nest territories year-round whereas others undergo seasonal movements to wintering areas (Berthold 1993). The evidence suggests that Northern Goshawks prefer mature forests for nesting, and that some individuals have winter home ranges that include their nest areas (Boal et al. 2003, 2005) and, as such, may have year-round preferences for mature forest. That said, the limited data on patterns of winter habitat use by migratory birds suggest that Northern Goshawks use non-forested as well as forested habitat once they leave their nesting territory.

Selecting and Measuring Environmental Features in Habitat Studies

Habitat characteristics. Biologists often measure many characteristics of the environment that are associated with the presence or absence or the abundance of specific organisms, and infer that these characteristics, or features to which they are related, are "life requirements" and important elements of habitat for these organisms. Vegetation, for example, can provide shelter for small mammals, which, in turn, provide food for raptors (Preston 1990, Madders 2000, Ontiveros et al. 2005). Because of this, it is important to determine which environmental features to measure before beginning a habitat study (Anderson and Gutzwiller 1994). Because there are many potential features to measure, and because it takes time to collect and analyze data, the number of features to be sampled must be limited. Choice of features to measure should be based on a thorough review of the literature on what is known about the species of interest (or close relatives), consultation with experts, and, in some instances, preliminary sampling (Anderson and Gutzwiller 1994). Features chosen should meet the objectives of the study, and be significant in terms of biological and conservation interest (Morrison et al. 1998, Morrison 2001, MacKenzie et al. 2006).

Habitat features that can be measured as part of a study of raptor habitat are numerous and vary with the kind of environment in which the study is conducted. Physiographic features such as slope, elevation, vegetation cover, distribution of water, human development, or soil type are relevant in many environments (Sutherland and Green 2004). In forest environments, species, size, density, and form of trees and vertical structure are common measures. Detailed measurements of raptor habitat in more open environments are less commonly described in the literature, but variables frequently include descriptions of ground vegetation, visibility, and the number of perches.

Techniques for measuring features of raptor habitats often are the same as those used by foresters, range managers, and other professional land managers. Employing widely used, standard techniques has two advantages: baseline information, collected with these techniques, already exists for many areas, and features of raptor habitat are expressed in terms familiar to land managers (Mosher et al. 1987). A disadvantage of land-management measurements is that many are arbitrary categorical variables used in one country or region (e.g., the U.S. Forest Service tree-density classes). As such, their use in raptor habitat studies limits comparisons across broad geographic areas and can reduce the likelihood of identifying habitat variables that are important range-wide (Penteriani 2002). In addition, management variables tend to be microscale variables, and additional methods generally are needed to obtain macroscale information (Oldemeyer and Regelin 1980, Bullock 1998, Morrison et al. 1998).

One important component of habitat structure is spatial heterogeneity or patchiness. This variable integrates not only absolute values of vegetation or physiography, but also their distribution in space. Habitat heterogeneity can be viewed at both coarse-grained (e.g. between cover types) or a fined-grained (within cover types) scales, and can be expressed in both vertical and horizontal dimensions. The choice of scale and the method for assessing heterogeneity or patchiness always should be organism-specific and should not be based on the perceptions of the investigator (Morrison et al. 1998). Many methods for measuring heterogeneity have been developed for use at a variety of scales (Anderson and Gutzwiller 1994).

Use versus availability. Studies of habitat preference and selection often necessitate designs and sampling schemes that assess available habitat, habitat not used, or the extent and manner of use by a species. For instance, biologists usually infer that certain features are available to a bird if the features in question occur within the individual's home range. In fact, investigators generally do not know if a bird is precluded from using certain features of the habitat due to phenomena not related to habitat (Cody 1981, 1985), including nest predation, interspecific competition, intra-specific attraction, and human disturbance (Newton 1998, Sutherland and Green 2004). The extent to which such phenomena affect both the habitat choices made by individuals and inferences drawn from correlative studies is unknown. Inferences about relationships among structural features of habitat (e.g., vegetation cover) and use of other features (e.g., prey) sometimes can be made by combining behavioral and habitat analyses (Bechard 1982, Bustamante et al. 1997, Selas 1997b, Thirgood et al. 2002, Amar and Redpath 2005). Inferences can be strengthened by experimentally manipulating features (e.g., prey, nest sites) hypothesized to be relevant to selection and monitoring the bird's response to this manipulation (Marcström et al. 1988). Finally, both the spatial and temporal scales of the study can influence the perception of habitat availability (Orians and Wittenberger 1991, Levin 1992, Anderson and Gutzwiller 1994, Sutherland and Green 2004).

Raptor populations and distributions. To assess the habitat needs of a species, researchers commonly study habitat use and infer selection or preference from it. Presumably, species should reproduce or survive better in habitats they prefer. This approach assumes that such preferences relate to fitness and, hence, to population growth (Garshelis 2000). Traditionally, measures of presence-absence and abundance have been considered appropriate surrogate measures for fitness in the study of habitat requirements of terrestrial vertebrates, including raptors (Litvaitis et al. 1994, MacKenzie 2005, but see Van Horne 1983). Because of recent analytical developments in modeling (Guisan and Thuiller 2005, MacKenzie et al. 2006), presence-absence data can be used in a variety of contexts, including identifying habitats that are of value to species of conservation concern (MacKenzie 2005). Because presence-absence data are easier to collect, they often are preferred over abundance data (Pearce and Ferrier 2001, MacKenzie 2005). The use of abundance data in habitat studies has advantages, however (Gibbons et al. 1994). A positive relationship between distribution and abundance has been demonstrated for numerous taxa, and this relationship has been used to evaluate the status of species of conservation concern (Kennedy 1997, DeStefano 2005). In areas where habitats for breeding are relatively scarce, the relationship between abundance and distribution appear to be less well defined (Venier and Fahrig 1996).

Assessing habitat quality. High-quality habitats for a given species presumably have the resources required to sustain relatively high rates of survival and reproduction. Directly measuring the required resources present in an area (e.g., number of prey items or nest sites) is one way to assess habitat quality, but it requires that resources needed by the species in question be known, and that the resources measured are available for use (see above). Another approach for assessing habitat quality is based on indicators of population health. As noted in the previous section, information on presence-absence and abundance of raptors is common in investigations of their habitats. However, the presence of a raptor in an area, although potentially indicating that the area constitutes habitat for that species, indicates little about its quality. In contrast, measures of abundance of a given species in an area often are indicative of the relative quality of the area as habitat, but may be misleading in some situations (Van Horne 1983), as measures of abundance alone cannot distinguish between habitat sources and sinks (cf. Pulliam 1988).

Perhaps the best indicators for assessing habitat quality for a given species are estimates of productivity and survival, or combinations of both (e.g., rate of population change, λ). Unfortunately, these measures are difficult to obtain in short-term studies. Estimating survival is especially problematic (e.g., Diffendorfer 1998) and usually requires monitoring marked animals (e.g., banded or radio-tagged) over extended periods. Yet the value of long-term banding programs is high, especially in assessing habitat quality, and they can be done at both small- (less expensive) and large- (more expensive) spatial scales.

One example of a long-term study of marked animals over a broad spatial scale involves the massive research effort focused on the Northern Spotted Owl (*Strix occidentalis caurina*) in the northwestern United States. Anthony et al. (2006) analyzed demographic data collected from 1985 to 2003 on Northern Spotted

Owls from 14 study areas, covering about 12% of the entire range of the subspecies, in Washington, Oregon, and California. The meta-analysis presented was based on 32,054 captures and re-sightings of 11,342 banded individuals, and was designed to assess population trends, and related issues of habitat quality, throughout the subspecies range. Obviously, this kind of research effort is rare, in part because of the high financial costs associated with such work. Such studies usually focus on high-profile threatened or endangered species.

Long-term banding programs also have been successful on relatively small spatial scales. For example, marking and monitoring Merlins (*Falco columbarius*) for 10 years in a single city, Saskatoon, Saskatchewan, Canada, allowed researchers to assess population viability (James et al. 1994) and lifetime reproductive performance in relation to nest-site quality (Espie et al. 2004). Similarly, marking and re-sighting Cooper's Hawks (*A. cooperii*) at 40 to 80 breeding sites for up to 10 years in another city, Tucson, Arizona, U.S.A., permitted examinations of questions about ecological traps (Boal 1997), source-sink dynamics (R. W. Mannan et al., pers. comm.), and natal-habitat imprinting (Mannan et al. 2007, unpubl. data).

APPLICATION

Raptor populations sometimes are limited at the microscale level (Bevers and Flater 1999) by the availability of breeding or roosting habitat (Newton 1979), and much research has been conducted on habitat use and preference of nest and roost sites (Thompson et al. 1990, Reynolds et al. 1992, Mañosa 1993, Cerasoli and Penteriani 1996, Gil-Sánchez et al. 1996, Iverson et al. 1996, Selas 1997a, Mariné and Dalmau 2000, Martínez and Calvo 2000, Finn et al. 2002, Penteriani 2002, Poirazidis et al. 2004, Squires and Kennedy 2006). Investigations of habitat associated with nesting activities that occur at larger spatial scales such as the PFAs (Daw and DeStefano 2001, McGrath et al. 2003), foraging areas (Bosakowski and Speiser 1994, Sergio et al. 2003, Boal et al. 2005, Tapia et al. 2007), and areas used during natal dispersal (Ferrer and Harte 1997, Mañosa et al. 1998, Balbontín 2005) are less common.

Below we illustrate how habitat has been measured in studies focusing on raptors and use examples from the finest scale, called activity points, working progressively through larger spatial scales, called activity sites, and activity areas.

Activity points. Nest structure and substrate during the breeding period is an example of an activity point that often is measured in studies of woodland raptors (Cerasoli and Penteriani 1996, Siders and Kennedy 1996, Selas 1997a, Reich et al. 2004). There are many measurements possible at nest trees, perches, roost sites, and foraging sites (Table 1). Locating these sites (i.e., activity points) in forested environments can be difficult and often requires intensive field observations (Rutz 2003, Leyhe and Ritchison 2004) or radio-telemetry that results in visual observations (e.g., Mannan et al. 2004). In non-forested habitats, finding sites where raptors hunt and perch is easier (Leyhe and Ritchison 2004), but researchers should not assume 100% detection, even in these open habitats (MacKenzie et al. 2006, P. Kennedy et al., unpubl. data).

Most, but not all, raptor studies in open habitats have focused on macroscale habitat measurements. A few have provided detailed microhabitat measurements surrounding activity points (Salamolard 1997, Martínez et al. 1999, Arroyo et al. 2002). For example, ledges or small caves on cliffs are important to many raptors during the breeding season (Cade et al. 1988, Donázar et al. 1989, Donázar et al. 1993, Ratcliffe 1993, Thiollay 1994, Carrete et al. 2000, Rico-Alcázar 2001, McIntyre 2002), and many characteristics have been measured and described at cliff sites (Table 1).

Habitat measurements also can be made at activity points outside of the breeding season. For example, measurements related to land-cover types (permanent pasture, crops, plowed, woodland) or different kind of perches (trees, poles, on the ground) (Plumpton and Andersen 1997, Canavelli et al. 2003) can be useful in explaining patterns of non-breeding habitat use.

Activity sites. Plots of various sizes surrounding activity points are examples of activity sites (Hubert 1993, McLeod et al. 2000). Physiographic features often measured in activity sites include forest structure and composition, elevation, slope, aspect, soil type, and distance to water and forest openings (Table 2). Some raptors perch on fence posts and roost and nest in buildings (Bird et al. 1996, Leyhe and Ritchison 2004), and distance to human dwellings also can be an important measure. Distance measures often extend beyond the bounds of measured plots, but are collected along with data at this scale.

Uncertainty about the relative importance of various habitat features can lead biologists to take many measurements at activity sites (Mosher et al. 1987). However, as mentioned above, a broad, "shotgun" approach to

Table 1. Variables that are regularly measured at raptor activity points in forests, open country, and at cliffs.

Variable	Comments and References
NESTS IN FORESTED HABITATS	
Stick nest or cavity	
Nest dimensions	Length, width, and depth (m) of the body of the nest and the nest cup (Lokemoen and Duebbert 1976, Schmutz et al. 1980).
Nest access distance	Measured as nest circumference minus sum of the diameters of support branches divided by the number of support branches (Bednarz and Dinsmore 1982, Morris et al. 1982).
Surface area of nest	Measured on the top of nest in cm^2 (Morris et al. 1982).
Nest volume	Measured both for the nest and the nest bowl in cm^3 (Morris et al. 1982).
Nest minus trunk difference	Distance between the nest and the main trunk estimated in m (Bednarz and Dinsmore 1982).
Number of supporting branches	(Bednarz and Dinsmore 1982).
Size of support branches	By size categories (Bednarz and Dinsmore 1982).
Cavity measurements	For variables related to cavity measures (cavity diameter, cavity depth, opening dimensions, opening exposure, number of tree cavities, etc.) see Korpimaki (1984) Mariné and Dalmau (2000), and Rolstad et al. (2000).
Visibility about point	
Nest concealment	Historically measured at the nest with a spherical densiometer, standard photograph, or categorical estimates (Moore and Henny 1983). Recent developments in image analysis may be useful (Ortega et al. 2002, Luscier et al. 2006).
Nest canopy coverage	Measure of the canopy coverage above the nest with a spherical densitometer (Moore and Henny 1983, Siders and Kennedy 1996). Recent developments in image analysis may be useful (Ortega et al. 2002, Luscier et al. 2006).
Vegetation openness above and around nest	Green and Morrison (1983).
Nest tree	
Point dbh	Diameter at breast height (dbh), measured in cm using a dbh tape or Biltmore (Morris et al. 1982, Hubert 1993).
Height of tree	Usually measured in m using a clinometer (Haga type altimeter) (Reynolds et al. 1982, Rosenfield et al. 1998).
Tree species	To describe usage or to determine preference (Rottemborn 2000).
Age of tree	Estimated using a site index table or increment borer (Tjernberg 1983, Selas 1996, Siders and Kennedy 1996, Selas 1997a).
Height of nest, perch, roost	Measured directly with a meter tape when in the tree banding young, or with a clinometer to the nearest tenth meter (Titus and Mosher 1981, Cerasoli and Penteriani 1996).
Percent nest height or relative nest height.	Calculated as nest height/nest tree height x 100 (Titus and Mosher 1981, Morris et al. 1982, Cerasoli and Penteriani 1996, Rosenfield et al. 1998).
Percent canopy height	Calculated as nest height/mean canopy height x 100 (Devereux and Mosher 1984).
Slope	Measured as a percent (Selas 1996, Rosenfield et al. 1998).
Elevation	Elevation of nest site (m) taken from altimeter, topographic maps or GIS database (Garner 1999).
Altitude category	Nest stand plots and control plots: assigned to the lower, middle or upper altitude zone (Selas 1996).
Nest-tree health	Estimated percent dead or diseased, or alive or dead (Moore and Henny 1983, Devereux and Mosher 1984).
Nest distance to	Landscape features that might influence nest preferences (Speiser and Bosakowski 1987, Iverson et al. 1996, Penteriani 2002). Typically measured in m or km.
Perch or roost point	
Perch type	Pole, tree, fencepost, windmill, etc (Preston 1980, Holmes et al. 1993).
Number of perches	Count of the number and types of perches in a given area (Janes 1985, Holmes et al. 1993).
Microclimate	Temperature, light, wind speed, etc. (Barrows 1981, Keister et al. 1985).

Table 1. *(continued)*

Variable	Comments and References
Perch or roost protection	Ranked variable for protection from the weather (Hayward and Garton 1984).
Distance to trunk	Distance from perch or roost point to trunk along limb (Hayward and Garton 1984).
Tree species, perch type	Description of substrate (Marion and Ryder 1975, Steenhof et al. 1980, Hayward and Garton 1984, Leyhe and Ritchison 2004).
Point dimensions	Similar to variables measured for nest trees (Steenhof et al. 1980).
Point distance to	Landscape features that might influence perch or roost preferences (Thompson et al. 1990, Rottenborn 2000). Typically measured in m or km.
NEST IN OPEN HABITATS	
Plant species at site	(Bullock 1998, Sutherland 2000).
Nest site visibility	Measuring the distance from which the nest contents are no longer visible along equally spaced transects from the nest (Simmons and Smith 1985, Amat and Masero 2004).
NEST ON CLIFFS	
Nest (or scrape) location	Describe as: on ledge, crevice, stick nests, in pothole or cave (Cade 1960, Ratcliffe 1993).
Nest location measurements	Length, width, height, depth of ledge or cavity (Squibb and Hunt 1983, Ratcliffe 1993).
Nest materials	Describe substrate: e.g., sand, gravel, dirt, vegetation, etc. (Cade 1960, Ratcliffe 1993).
Rock type	Describe (e.g., granite, shale, soil, etc.) (Cade 1960, Ratcliffe 1993, Gainzarain et al. 2002, Hirzel et al. 2004).
Overhang	Categorize and describe (e.g., overhang > 90° vertical, open <90°) (Squibb and Hunt, 1983), or use a tape measure and clinometer to measure size and angles.
Vegetation near nest	Describe type and proximity of plants to nest (scrape) (Ratcliffe 1993).
Vegetation, plant community at base of and at top of clif	List species or describe community (Cade 1960, Ratcliffe 1993, Martínez and Calvo 2000, Martínez et al. 2003).
Nest height on cliff (or percent nest height) and above water	Measure (meter tape, rope length, transit, photographic comparison with topographic maps) or estimate (Cade 1960, Burnham and Mattox 1984, Donázar et al. 1993).
Distance from top (brink) and base of cliff to nest	Measure or estimate (Cade 1960, Ratcliffe 1962, Ratcliffe 1993).
Exposure of nest	Direction that nest (scrape, opening) faces (Ratcliffe 1962, Ratcliffe 1993).
Altitude of cliff	Height of site above sea level, often taken from topographic maps (Ratcliffe 1962, Burnham and Mattox, 1984, Gainzarain et al. 2002).
Orientation of cliff	Direction (aspect) the cliff faces, measure with compass (or estimated from topographic map) as angle perpendicular to main cliff face (Ratcliffe 1962, Donázar et al. 1993).
Height and length of cliff	Can be measured using meter tape, rope, distance and angle height with clinometer, range finder, or from topo graphic maps or air photo) or estimated and placed in categories (Ratcliffe 1993, Ontiveros 1999, Martínez and Calvo 2000).
Cliff relief	Highest point on cliff minus lowest point (Donázar et al. 1993).
Slope of cliff	Measure (clinometer) or place in categories (e.g., >90°, 80–90°, etc.) (Ratcliffe 1962, Ratcliffe 1993).
Relation of cliff to surrounding topography	General description (Ratcliffe 1993, Martínez and Calvo, 2000).
Distance and direction across valley, height (slope) of opposite valley	Estimate in field or use topographic maps (Donázar et al. 1993) or GIS.
Distance to human activity	Estimate in field or use topographic maps (Donázar et al. 1993, Ratcliffe 1993, Ontiveros 1999, Martínez and Calvo 2000) or GIS.
Distance to the nearest-neighbor nest	Estimate, or use topographic maps (Gil-Sánchez et al. 1996, Martínez and Calvo 2000) or GIS.

Table 2. Vegetation structure and floristic variables measured at raptor activity sites in wooded habitat.

Variable	Comments and References
Plant species richness, diversity index	Record the plant species within a plot (Titus and Mosher 1981) accounting for detectability (MacKenzie et al. 2006).
Tree species importance values	Record tree species relative density and frequency to compute importance values (Morris and Lemon 1983).
Tree-stem density by size, class, and species	Measured directly by recording the dbh of all trees in the plot by species. Provides data from which different size classes may be constructed or importance values calculated (Titus and Mosher 1981, Morris and Lemon 1983, Selas 1996, Selas 1997a). Plotless sampling techniques will provide estimates of some of the same information (Reynolds et al. 1992, Siders and Kennedy 1996).
Shrub and understory density	Either estimated by an index or census the plot according to dbh or height criteria (Titus and Mosher 1981, Morris and Lemon 1983, Rosenfield et al. 1998). Numerous techniques are available (Oldemeyer and Regelin, 1980, Bullock 1998).
Distance between trees (m)	(Siders and Kennedy 1996, Penteriani and Faivre 1997).
Tree density	Number of trees per hectare (Rosenfield et al. 1998, Garner 1999), or by size class (Siders and Kennedy 1996).
Mean dbh	Mean diameter (cm) at breast height of trees in study plot (Mañosa 1993, Rosenfield et al. 1998).
Basal area (m^2/ha)	May be calculated from tree dbh per unit area (Morris and Lemon 1983, Mañosa 1993, Cade 1997, Rosenfield et al. 1998) or estimated using an angle gauge.
Tree height class	Tally of trees by height class (see revision of Penteriani 2002).
Tree structure class	Used to classify dead or dying trees (Devereux and Mosher 1984, Selas 1996).
Crown volume	Determines volume by height and shapes categories (Moore and Henny 1983).
Crown depth	Expressed as a percent of tree height (Reynolds et al. 1992).
Tree strata	Discrete number of layers of canopy and understory (Reynolds et al. 1992).
Canopy volume (m^3)	(Penteriani and Faivre 1997).
Canopy cover	Measure of area potentially covered by multiple trees due to crown overlap. Typically expressed as percent cover (Reynolds et al. 1982, 1992, Penteriani and Faivre 1997).
Closure of canopy, understory, ground cover	Estimated using a GRS densitometer (K. A. Stumpf, unpubl. data). Recent developments in image analysis may be useful (Ortega et al. 2002, Luscier et al. 2006).
Percent cover in perch stand	Similar to variable measured for nest stand (Leyhe and Ritchison 2004).
Tree density in perch stand	Similar to variable measured for nest stand (Leyhe and Ritchison 2004).
Vegetation height in perch stand	Height of total ground and shrub vegetation surrounding point in m (Leyhe and Ritchison, 2004).
Vegetation profile	A density board may be used to estimate the amount of vegetation at height intervals (Nudds 1977, Bullock 1998). Numerous variables and categories can be created or more quantitative approaches can be used (Blondel and Cuvillier 1977).
Inter-tree heterogeneity	Index of mean inter-tree distance and variability (Roth 1976).
Horizontal diversity and habitat heterogeneity	For examples and methods see Litvaitis et al. 1994.

data collection may not be the best design strategy. Variable selection should be based on the study objectives, and should be significant in terms of biological and conservation interest. Variables that often describe significant features of nest sites of woodland raptors include tree-stem density by size class, canopy closure and basal area (Selas 1996, Siders and Kennedy 1996, Daw and DeStefano 2001). These measures usually relate to stand age. Shrub and ground cover variables, which are considered less important (but see Boal et al. 2005), may characterize significant features around hunting perches (Farrel 1981, Leyhe and Ritchison 2004).

The choice of sample plot size, shape, and distribution is fundamental to field studies and the raptor-habitat literature illustrates many choices. Size of plots can vary from 0.04 ha (Armstrong and Euler 1982, Siders and Kennedy 1996, Rosenfield et al. 1998) to 0.75 ha (Tjernberg 1983, Poirazidis et al. 2004) to 64 ha (P. Kennedy et al., unpubl. data).

Activity areas. Activity areas are similar to activity sites, but encompass larger areas. For example, an activity area might be identified as a plot large enough to include a substantial portion of a home range (e.g., a 1-km radius). Habitat features measured in activity sites also can be measured in activity areas (McGrady et al. 2002, Bosch et al. 2005, Tapia et al. in press), although measures taken in activity areas tend to be coarser. For example, vegetation in activity areas might be described by listing dominant plants or proportional coverage of vegetative communities. Areas also could be described by proportional coverage of land-use or land-cover types (Mosher et al. 1987, Table 3).

Table 3. Physiographic, land-cover, and land-use type variables measured at raptor activity sites and areas.

Variable	Comments and References
Altitude	Measured using a surveying altimeter or topographic map (Donázar et al. 1993, Penteriani and Faivre 1997, Martínez et al. 2003), or obtained from analysis of the variable using a digital elevation model with digital cartography and GIS (Tapia el al. 2004, López-López et al. 2006).
Slope gradient in degrees, and slope exposure (%)	Measured with clinometer, abney rule, or level; (Titus and Mosher 1981, Reynolds et al. 1982, Penteriani 2002); or obtained from analysis of the variable using a digital-elevation model with digital cartography and GIS (Tapia et al. 2004, López-López et al. 2006).
Aspect	The direction toward which a point or site faces; the direction away from the slope; the direction of most open vegetation (Titus and Mosher 1981, Reynolds et al. 1982, Selas 1996).
Type of water	Categories (temporary versus permanent, stream, river, pond, lake, size categories, 1 ha, 1.1-5 ha, etc.) (Reynolds et al. 1982).
Distance to water or other landscape feature	Measurement with a tape or paced; can record as seasonal water or permanent (Morris and Lemon 1983); or obtained from analysis of the variable using a digital elevation model with digital cartography and GIS.
Soil-woods or land productivity index	See Newton et al. (1981) for examples relating raptor use to land cover and land productivity indexes.
Land cover or land use	Probably the most commonly obtained set of macro-variables in raptor habitat studies. Usually categorized by general habitat type at the activity site (e.g., pasture, cropland, woodlot, water, field/forest edge). Used in many studies (see Bullock 1998, Sutherland and Green 2004).
Amount of land cover	Measured in ha, km^2 or categories. May be delineated based on habitat use as determined by radio-telemetry (Selas and Rafoss 1999, Newton 1986), direct observation (Tapia et al. 2004), or indirectly by measuring plots delineated by home range boundaries or circles centered on a point (Moorman and Chapman 1996).
Relief index	An index of topographic variation based on the number of contour lines crossed by transects radiating from activity point (González et al. 1990, Donázar et al. 1993).
Baxter-Wolfe interspersion index	Determines the number of changes in habitat type occurring along transects (Litvaitis et al. 1994).
Area of cover type	Satellite imaging involves computer-driven interpretation of available satellite images. The resolution of these images is determined by pixel size (Andries et al. 1994).
Human disturbance	Number of and distance to human settlements, buildings, roads, etc. (Tapia et al. 2004, 2007, Balbontín 2005).
Cover-type and prey-base associations	Index of abundance of prey associated with cover types and raptor use (Bechard 1982, Thirgood et al. 2003, Ontiveros et al. 2005).

The rapid development of remote-sensing techniques and Geographic Information Systems (GIS) has facilitated handling and management of environmental data at increasingly larger spatial scales (Koeln et al. 1994, Bullock 1998, Corsi et al. 2000). Remote sensing is useful for collecting macrohabitat features of activity areas, such as slope, elevation and other physiographic features. However, it does not replace field observations because many vegetation variables (e.g., stand structure, range condition) cannot be obtained accurately from remotely sensed data. Even for measurements that can be measured accurately with remotely sensed data, ground truthing is required to quantify the level of accuracy for a particular landscape.

Prey abundance. Prey abundance and availability are known to limit raptor populations (Newton 1979, Newton 1998, Dewey and Kennedy 2001). As a result, raptor habitat requirements often are linked to the distribution of their prey. Because it is difficult to observe predatory behavior in most raptors, the influence of prey on habitat use by raptors often is inferred by comparing, typically at the scale of activity areas, measures of prey abundance and raptor use among categories of vegetation or land use (Graham and Redpath 1995, Marzluff et al. 1997, Selas 1997b, Bakaloudis et al. 1998, Ontiveros et al. 2005). Use of land or vegetation types by raptors often is positively associated with prey abundance (Selas and Steel 1998, Ontiveros et al. 2005), but such relationships can be confounded by density of vegetation. That predation is sometimes more intense in areas where vegetation is less dense, regardless of prey abundance (Bechard 1982, Thirgood et al. 2003, Ontiveros et al. 2005) illustrates the need to distinguish, whenever possible, prey abundance from prey availability (Mosher et al. 1987).

DATA ANALYSIS

Statistical methods by which habitat preference is inferred are highly variable and differ in their precision and applicability (Alldredge and Ratti 1986, 1992, Titus 1990, Manly et al. 1993, MacKenzie et al. 2006). Analytical techniques for examining the multivariate nature of wildlife-habitat relationships (Corsi et al. 2000) include Generalized Linear Models, Bayesian approaches, classification trees and multivariate statistical methods such as Multiple Regression, Canonical Correlation Analysis, Principal Component Analysis, and Discriminant Function Analysis (Donázar et al. 1989, Kostrezewa 1996, Morrison et al. 1998, González-Oreja 2003).

Habitat features may have linear or nonlinear effects and these effects can be additive or multiplicative on the abundance of a species. Analytical techniques that enable examination of complex associations may be desirable over methods that assume simple linear relationships (e.g. simple correlation). On the other hand, inadequate sample size and many predictor variables often are problems when multivariate methods are used (over-parameterized model) (Morrison et al. 1998). Interpretations based on complex models and inadequate samples can be misleading. Required sample sizes largely are related to existing variation in the system being studied and effect size, but a crude estimate of the minimum sample size needed for multivariate analyses is 20 observations, plus 3 to 5 additional observations for each variable in the analysis. Morrison et al. (1998) suggested that an additional 5 to 10 observations for each variable provide a more conservative target for an adequate sample size. Even so, large sample sizes do not compensate for poorly designed studies or biased sampling. Recently, many biologists have shifted away from using statistical significance (and arbitrary or *a priori* p-values) as the defining point for biological significance and instead develop multiple, competing *a priori* models which are then evaluated by model selection techniques such as Akaike Information Criterion (AIC) (Anderson et al. 2000, Jongman et al. 2001). Whatever approach is adopted, the requirements and limitations of the statistical techniques employed should be understood before embarking on such a study (Manly 1993, Morrison et al. 1998).

Modeling the distribution of raptors and other vertebrate species (i.e., generating atlases) has become more common in recent years (Bustamante 1997, Sánchez-Zapata and Calvo 1999, Sergio et al. 2003, Rushton et al. 2004). Although the value of such atlases is somewhat limited (Donald and Fuller 1998, Sutherland 2000), they can be useful in predicting the presence of a species, and often play a role in assessing habitat suitability (Osborne and Tigar 1992, Tobalske and Tobalske 1999, Jaber and Guisan 2001, Bustamante and Seoane 2004, Tapia et al. 2004, in press). To illustrate this, we use an example where both the historical and present distributions of Golden Eagles (*Aquila chrysaetos*) were modelled in the province of Ourense (7,278 km^2, southeast of Galicia in northwestern Spain).

Current distribution of eagles was estimated by searching the province for breeding pairs each spring from 1997 to 2002. The historical distribution was estimated by reviewing available published information, as well as historic field data provided by biologists and gamekeepers. Several environmental variables were selected to model habitat attributes, namely land use, degree of humanization, topographic irregularity, and habitat heterogeneity. These parameters were represented on a 10-km^2 grid. Values for these environmental variables were obtained from 1:50,000 digital cartography with the aid of GIS software. The distribution of Golden Eagles was modelled for three periods: current (1997-2002), historical (the 1960s and 1970s), and current and historical periods pooled. Stepwise logistic regression analysis was then performed for each period with presence-absence of Golden Eagle as the dependent variable. It was assumed that the distribution of the Golden Eagle in Ourense is known with full precision, with no false absences (Hirzel et al. 2002, Bustamante and Seoane 2004). At the spatial scale considered, the best predictors of habitat suitability for breeding were topographical variables indicative of rugged relief. Cartographic models derived from these analyses showed estimated probability of occurrence of eagles within each 10-km^2 grid square.

The model allows managers to: (1) simulate the effects of silviculture, mining or fires within each grid, thus enabling effective assessment of environmental impacts; (2) identify shrublands to manage for enhancing prey density and prey availability; (3) annually identify areas to monitor for the presence of potential hazards for Golden Eagles (e.g., wind farms, power lines, etc.); (4) regulate outdoor recreation potentially hazardous for eagles; and (5) catalog the cliffs and rocky outcrops potentially suitable for nesting. Information about the location of nesting areas must be updated annually to allow the generation of new models, predict range expansions or contractions or identify suitable sites for reintroductions, and provide a basis for design of protected areas.

CONCLUSIONS

We conclude with a quotation from the first version of this work that remains as true today as it was in 1987: *"As evidenced by the recent literature, raptor habitat research is becoming more rigorous. Questions require more accurate and precise answers, and statistical support is mandatory in many cases, whether the objectives are ecological interpretation or application to management. Manuscripts and reports to agencies will be subjected to increasingly critical review of methodology and statistical analyses. Because of sample size problems and regionally limited applicability, researchers should consider opportunities for collaborative studies, and adopt proven techniques and measurements. Comparability of data will increase their value and make it possible to apply more complex statistical analyses to large, shared data bases"* (Mosher et al. 1987:93).

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