CHAPTER 2

THE HABITAT CONCEPT IN ORNITHOLOGY

Theory and Applications

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1. INTRODUCTION

Ornithologists have played a key role in the development of the habitat concept. The conspicuous nature of birds has allowed ornithologists to assemble a vast amount of information relating the distribution and abundance of birds to aspects of the environment (Brown, 1984; Mayr, 1988; Konishi et *al.*, 1989; Morrison et *al.*, 1992). The application of the term "habitat" has been used as a unifying, theoretical concept to explain the diversity of avian life-history patterns (Rotenberry, 1981). However, specific definitions of the term "habitat" are often vague. Definitions have ranged from, for example, how species are associated with broad, landscape-scaled vegetation types, to very detailed descriptions of immediate physical environments used by species (Karr, 1980; Verner et *al.*, 1986; Harris and Kangas, 1988).

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Current Ornithology, Volume 11, edited by Dennis M. Power. Plenum Press, New York, 1993

Confusion over the use of the term "habitat" has resulted in considerable ambiguity regarding its meaning. This confusion has been compounded by additional terminology, (e.g., macrohabitat, microhabitat, critical habitat, core area, habitat use, habitat association, habitat selection, habitat preference, habitat suitability, and habitat quality) that builds on this relatively ambiguous concept. A common thread, however, among different definitions and terms is that "habitat" relates the notion of presence of a species to attributes of the physical and biological environment (Morrison et *al.*, 1992).

Confusion also exists over the distinction between habitat and niche (Whitaker et al., 1971). Whereas our objective is not to continue this debate, we recognize a need to arrive at a clear understanding of what each term entails to foster an unambiguous communication of the topic at hand. Thus, we will adhere to the following framework throughout our discussion. We regard niche from a Grinnellian perspective (James et *al.*, 1984), and consider it to be the suite of biotic and abiotic factors that permit an animal to use part of the environment. Niche also includes the manner (e.g., behavior) in which a species exploits this subset of the environment. We restrict our definition of habitat to the subset of physical environmental factors that a species requires for its survival and reproduction. As such, habitat is essentially imbedded within the niche. Habitat and niche are therefore not mutually exclusive concepts. Each is closely intertwined with the other and can be modeled using the multidimensional approach developed by Hutchinson (1957).

Our objectives are to: (1) review the history of the habitat concept with a special emphasis on scale-dependency of habitat descriptions; (2) review theoretical and applied approaches to the study of birds and their habitats; and (3) discuss the management of habitats using case histories from the ornithological literature. We will address these objectives from the standpoint of what is known about relationships between birds and their habitats and propose directions for future work. We acknowledge that our discussion of this topic will not be exhaustive. Rather, we regard this chapter as a forum that will stimulate ornithologists to reconsider habitat ecology as a unifying concept. Our approach is to provide an overview of the theoretical and applied uses of the term to summarize the current status of the habitat concept, and to promote a consistent direction for future ornithological studies.

2. HISTORICAL PERSPECTIVE

Odum (1971) referred to habitat as the "address" of the organism. Whether that address refers to a city, neighborhood, zip code, block, house, or room within a house is where much of the confusion abounds about the specific definitions of habitat. MacMahon et *al.* (1981) regarded habitat as an artificial, human construct to describe where an animal occurs. We do not argue with them, but acknowledge that most of what we know regarding the ecology of free-ranging organisms is somewhat artificial. Essentially, researchers attempt to describe a species' habitat from a human perspective by correlating features of the environment to the presence or relative abundance of the organism. Hopefully, this description has some relevance to those factors that the species actually uses and requires for its persistence.

2.1. Permutations of the Term "Habitat"

The term "habitat" has been used variously by ornithologists to relate birds to aspects of the environment. Many of these permutations can be attributed to different scales of observations (Fig. 1). Johnson's (1980) hierarchical approach to habitats is based on viewing selection at different spatial scales. For example, spatial scales can range from considering the use of a specific perch or foraging substrate to listing biomes within the geographic range of the species. Temporal descriptions can include environments used seasonally (e.g., breeding, wintering, migratory), yearly, or historically. Confusion is compounded when the term "habitat" is used in political arenas. The Endangered Species Act of 1973 includes a provision for "critical habitat." Whereas biologists might provide very eloquent descriptions of what "critical habitat" should provide, objective criteria for clearly defining the "critical habitat" of a species are often lacking.

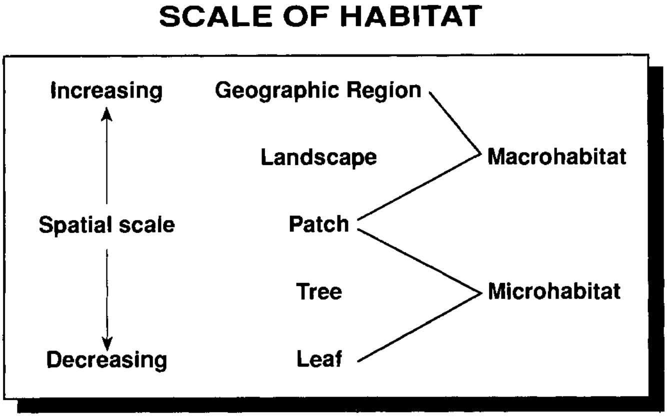

FIGURE 1. Continuum of spatial scales for the study of avian habitats.

To provide a common framework, we propose that the following definitions be used. Our purpose here is not to become engrossed in a semantic argument, but to outline some basic working definitions so that terms relating to habitat can be used consistently and unambiguously.

Habitat use: The manner in which a species uses a collection of environmental components to meet life requisites. Habitat use can be regarded in a general sense, or broken into specific acts or needs such as foraging, nesting, or roosting.

Habitat *selection/preference:* Innate and learned behavioral responses of birds that allow them to distinguish among various components of the environment resulting in the disproportional use of environmental conditions to influence survival and ultimate fitness of individuals.

Habitat suitabilitylquality: The ability of the environment to provide conditions appropriate for survival, reproduction, and population persistence. Suitability is a continuous variable measured by the intrinsic rate of population increase.

Macrohabitat: Landscape-scaled features that are correlated with the distribution and abundance of populations. Often used to describe seral stages or discrete arrays of specific vegetative types.

Microhabitat: Specific, recognizable features of the environment that act as proximal cues to elicit a settling response from an individual bird.

Critical habitat: ". . . physical or biological features (I) essential to the conservation of the species and (II) which may require special management considerations or protection . . ." (United States Government Printing Office, 1983:2).

2.2. Historical Overview

The study of avian habitats falls broadly into three overlapping eras: (1) the catalog era, (2) the qualitative natural history era, and (3) the quantitative ecology era (Karr, 1980) (Fig. 2). The transition from one era to the next represents a major increase in the cumulative knowledge and comprehension by ornithologists of how birds are related to their environments (Fig. 2). For example, the theories and ideas of Charles Darwin provided the impetus for the move from the catalog to the natural history era, and the transition from the natural history to the mathematical ecology era was largely influenced by G. Evelyn Hutchinson and Robert MacArthur. Our primary focus in this historical overview will emphasize applied concepts and techniques that pertain to the quantitative ecology era. However, a brief historical sketch on how early studies of avian habitat relationships were approached is essential for understanding the merits and limitations of contemporary studies.

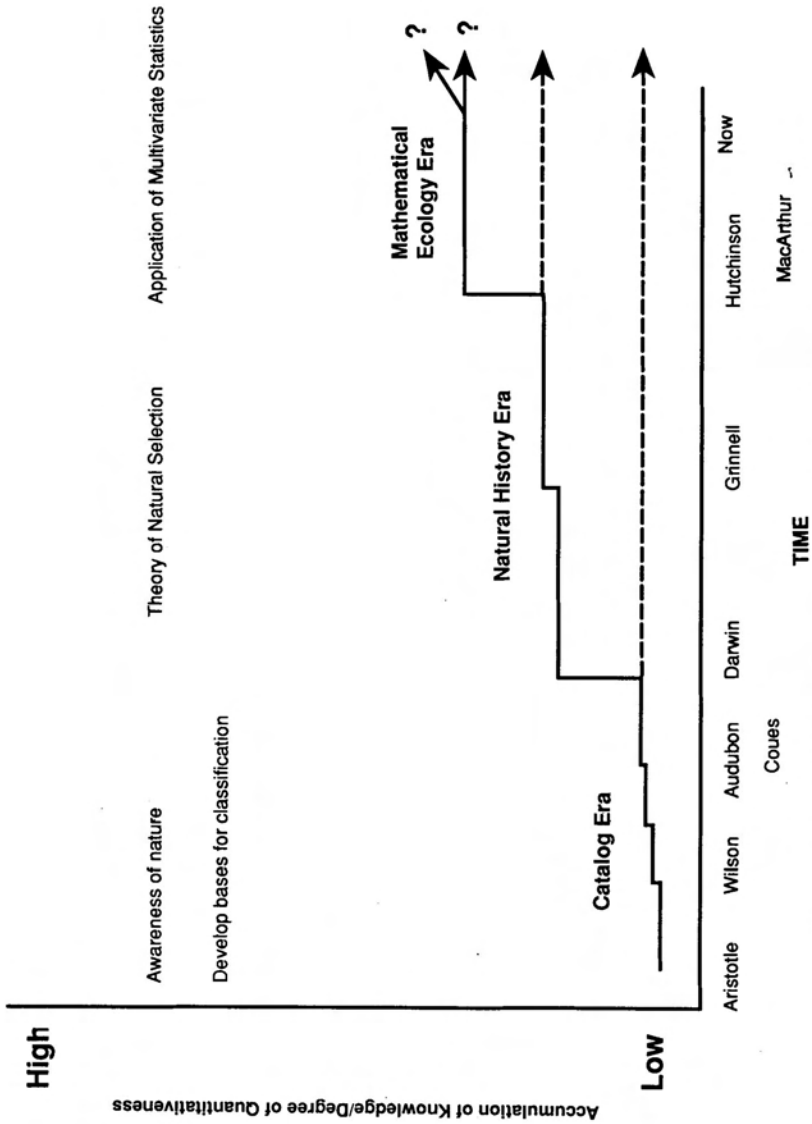

FIGURE 2. Historical development of the habitat concept in ornithology.

2.2.1. The Catalog Era

The catalog period in studies of avian-habitat relationships essentially began with Aristotle (Mayr, 1982; Morrison et *al.*, 1992) and continued until the early twentieth century. During this broad span of time, ornithologists were concerned primarily with making basic associations between specific birds and particular environments, described in general terms (e.g., Baird et *al.*, 1874, 1884; Coues, 1874). In North America, the catalog era was initiated by Alexander Wilson's systematic collection and cataloging of avian specimens. This tradition was adopted and continued by John J. Audubon. As westward expansion gained momentum during the mid-nineteenth century, Elliot Coues and Charles Bendire, surgeons in the Army Medical Corps, continued to collect avian specimens and record basic notes on the environments at collection sites. By the 1870s, most known species of birds had been described by these early naturalists. Thus, ornithologists shifted their focus from collecting and describing new species to collecting and describing new subspecies or "trinomials." Further, Darwin's ideas about natural selection (Darwin, 1859) induced ornithologists to consider the evolutionary basis for relationships between birds and their habitats.

2.2.2. The Qualitative Natural History Era

Keen insight and synthetic analyses of Joseph Grinnell were crucial in moving the ornithological community from the cataloging era to one dominated by qualitative descriptions of natural history. Grinnell was largely responsible for redirecting the study of birds and their environments from a simple cataloging approach to one dominated by a synthesis of ideas about processes that were responsible for the distribution and abundance of birds. Much of Grinnell's philosophy of nature was based on applied Darwinism (Miller, 1943), and clearly was centered on hypotheses concerning vertebrates (primarily birds) and their evolutionary relationships with the environment. For example, his speculation about factors responsible for the distribution of the Chestnut-backed Chickadee (*Parus rufescens*) in relation to humid coastal forests (Grinnell, 1904) is classic. Nearly 80 years later, it still provides an explanation for a subsequent large-scale range expansion of this bird (Brennan and Morrison, 1991). Grinnell's lasting contribution was that he posed some testable and untestable hypotheses about factors that potentially influenced habitat distributions of birds. Life history attributes, such as nesting success, presence or absence of foraging or roost sites, and seasonal differences in habitat use, were all part of Grinnell's scheme of habitat description (Grinnell et *al.*, 1918;

Grinnell and Miller, 1944). Unfortunately, he never lived to complete the text for his outline of Geography and Evolution (Miller, 1943), a book that would have provided a broad organic synthesis based on his extensive work with birds and their habitat relationships in western North America. Nevertheless, Grinnell's work on birds and their habitat relationships made a permanent impact on how ornithologists approached habitat analyses during this period of qualitative natural history. Grinnell's ideas and approach to science also set the stage for the current era of quantitative habitat ecology in which we are presently immersed. Empirical work and syntheses by Herbert Stoddard (1931), David Lack (1933), and Aldo Leopold (1933) suggested even further that it should be possible to predict presence/absence and abundance of birds based on information about their habitat.

2.2.3. The Quantitative Ecology Era

The combined influence of G. Evelyn Hutchinson and Robert MacArthur was largely responsible for shaping the contemporary approach to the study of birds and their habitats. Hutchinson's concept that a multidimensional ecological niche (Hutchinson, 1957) could be quantitatively described furthered the notion that species' distributions were determined by a suite of biotic and abiotic factors acting synergistically. MacArthur, a student of Hutchinson, possessed a strong analytic background and was able to apply rigorous quantitative methods to describe, test, and predict these ecological patterns. Perhaps MacArthur's primary contribution was his ability to quantify and elucidate in a simple way subtle and sometimes complex differences in habitat-use patterns of birds. For example, MacArthur's (1958) seminal work on eastern wood warblers inspired a subsequent generation of ornithologists to apply this approach to their favorite groups of birds and other animals (e.g., Cody, 1968; James, 1971; Noon, 1981a).

There was about a 10-year "lag" between the publication of MacArthur's dissertation (MacArthur, 1958) and the application of multivariate statistics in studies of avian habitat relationships. The mathematical genius of Robert MacArthur and the advent of digital computers were two key factors that clearly shaped how contemporary habitat ecologists approached analyses of relationships between birds and habitat factors. The tremendous computational burden of complex quantitative analyses was eliminated by the digital computer. After some additional key methods papers were published (Cody, 1968; Klebenow, 1966; James and Shugart, 1970; James, 1971), the quantitative approach to analysis of avian habitat relationships was clearly underway.

3. THEORETICAL FRAMEWORK OF THE CONTEMPORARY HABITAT CONCEPT

The distribution and abundance of a species is bound by its physical limitations (Liebig, 1841; Shelford, 1913). Within these limits, actual habitat use by a species is further influenced by its density, densities of and interactions with other species, resource abundance and distribution, and various other biotic and abiotic factors. Rarely, if ever, does an individual use the full range of environments within its capabilities. Thus, habitat use and selection are complex processes influenced by morphological and physiological adaptations of a species and its innate and learned behavioral responses to external and internal stimuli.

3.1. Theory of Habitat Selection

Rosenzweig (1985) argued that habitat selection theory was a subset of optimal foraging theory. We contend, however, that foraging theory is actually a subset of habitat theory, because animals use habitats to meet numerous other life history needs (e.g., breeding, roosting, loafing) besides foraging alone. Much of the optimal foraging literature predicts the use of patches of various sizes containing different quantities and qualities of food resources (Pyke et *al.*, 1977; Pyke 1984). Unfortunately, optimality modeling has scarcely addressed topics that go beyond foraging-patch selection. Nevertheless, the notion of habitat as the place containing resources needed for survival and reproduction is clearly central to any theoretical consideration of the habitat concept.

Southwood (1977) theorized that characteristics of a habitat acted as a "templet" that influenced ecological strategies used by animals to survive and reproduce. Building on concepts developed by Burges (1960), Birch (1971), and Taylor and Taylor (1977), Southwood used a simple, two-dimensional "reproductive success matrix" to represent time and space. His template analogy is a unifying, theoretical framework for habitat ecology that clearly is rooted in the theory of natural selection. Although most of Southwood's examples were from the entomological literature, much of his theoretical constructs are directly relevant to birds and other organisms. For example, reproduction and survival of an organism can be cast in a matrix and used to calculate the probabilities of reproductive success at different points in space and time (Fig. 3).

The notion of temporal and spatial habitat heterogeneity in both time and space (May, 1974) plays a prominent role in Southwood's theoretical framework. That is, the abilities of a habitat to provide necessary resources for an individual to survive and ultimately to reproduce are unequal in time and space. Spatial variations largely result from stochastic events that

	A	TIME	
		Now	Later
SPACE	Here	r_a	r_b
	Elsewhere	r_c	r_d

	B	TIME	
		Now	Later
SPACE	Here	E_a	E_b
	Elsewhere	E_c	E_d

	C	TIME	
		Now	Later
SPACE	Here	V_a	V_b
	Elsewhere	V_c	V_d

	D	TIME	
		Now	Later
SPACE	Here	$E_a(r_a \pm V_a)$	$E_b(r_b \pm V_b)$
	Elsewhere	$E_c(r_c \pm V_c)$	$E_d(r_d \pm V_d)$

FIGURE 3. Matrix models of habitat relationships in time and space adapted from Southwood (1977). (A) Matrix of favorability where r = potential rate of increase according to different strategies; (B) expectancy of "being there" or surviving in time and/or space; (C) risk matrix (variance of r in time and space); (D) reproductive matrix showing number of descendants resulting from each strategy.

act uniquely across the landscape (Gleason, 1926), resulting in different arrangements of resources among specific locations. Temporal variations result from natural change such as vegetation succession seasonality, fire, flood, or weather, or from anthropogenic change such as agriculture, urbanization, or water development. Regardless of the underlying cause, it is critical to recognize that the environment changes constantly resulting in unique arrangements of resources and, hence, different habitats. In Southwood's scheme, relatively permanent habitats should exhibit little variance in "favourability," whereas ephemeral habitats should exhibit greater variation in "favourability" (Fig. 3). "Favourability" is analogous to Van Horne's (1983) concept of "habitat quality" inasmuch as they both relate rates of survival and reproduction to particular environments. Southwood (1977) expressed favorableness of a habitat as the mean rate of increase (r) achieved by a population. He acknowledged that r was directly dependent on resource abundance (or carrying capacity, K) and population density. Southwood (1977:359) emphasized that habitat was not "a rigid causal template . . . in the engineering sense." He argued that organisms may evolve to exploit different "templets," and that organisms can directly modify their own habitat through grazing and other forms of resource consumption. Thus, habitats and organisms are ultimately linked in a form of feedback that must be perceived as a dynamic system. The templet, or habitat, merely provides the basic outline of the relationships between an organism and its environment, and provides a theoretical starting point for assessing these relationships. Perhaps the greatest value of Southwood's reproductive success matrix is that it defines and quantifies aspects of the environment that influence the reproductive success of an organism.

The contribution of a habitat to the fitness of an individual, commonly termed habitat suitability, will vary in time and space. Suitability can be regarded as a continuous variable corresponding to spatial and temporal variations of environmental conditions. Fretwell and Lucas (1970) hypothesized that in an "ideal" situation, a species would use the habitat of highest suitability first, and then expand its distribution to use secondary habitats with increasing population size. Fretwell and Lucas's (1970) ideal-free model rests on three basic assumptions: (1) habitat suitability decreases with increasing bird density; (2) birds select the habitat that will confer the greatest fitness; and (3) birds are free to enter any habitat. At low populations, birds will enter the habitat of highest suitability (S, in Fig. 4A). Once the population level reaches the point where the suitability of habitat 1 equals the basic suitability (B,) of habitat 2, it would be advantageous for a proportion of the birds to use habitat 2. Territorial behavior, however, also influences habitat suitability by reducing the amount of suitable habitat available. The ultimate consequence of territoriality is to accelerate the decline of suitable habitat, hence making the selection of alternative habitats even more appealing (Fig. 4B).

Johnson (1980) proposed that habitat selection could be viewed within a hierarchical framework. He defined first-order selection as the physical or geographic range of the species. Within the geographic range, individuals or social groups use home ranges that constitute second-order selection. The use of a specific site within the home range defines third-order selection. Fourth-order selection entails the procurement of actual resources (e.g., food) from that site. This framework for habitat selection is not just restrictive to areas where birds breed. It is also applicable to areas that birds use during winter or migration, for example. Hutto (1985) applied this conceptual model of habitat selection to migrating warblers (Fig. 5). He concluded that first-order selection was probably innate and inflexible, whereas second- and third-order selection involved decision-making processes—processes that he concluded were mostly influenced by food availability.

Clearly, selection and use of the appropriate habitat over time and space enhance the probability of survival and therefore influence fitness

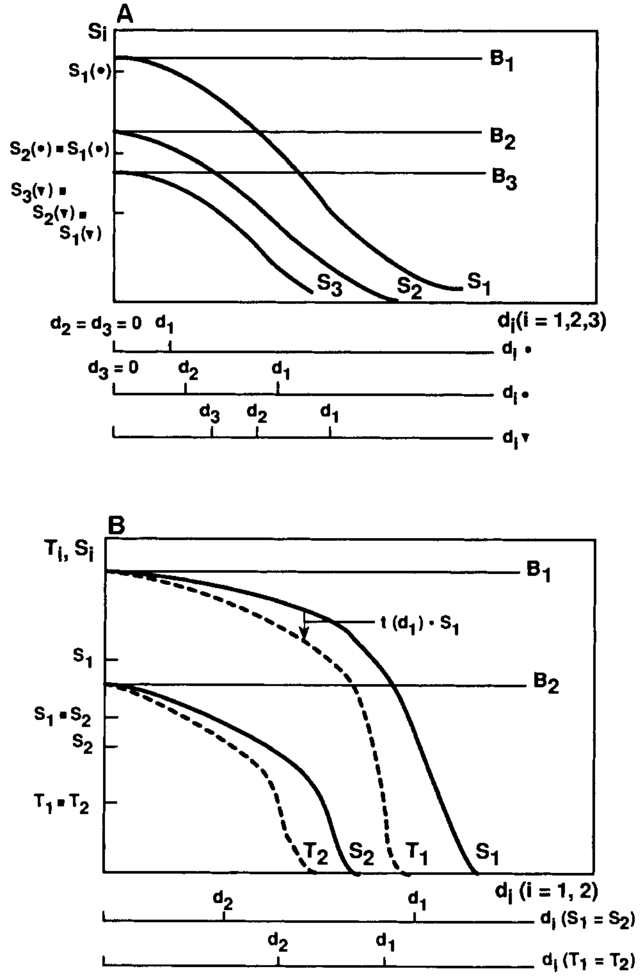

FIGURE 4. (A) Relationship between habitat suitability and bird density in an "ideal free" situation. (B) Relationship between habitat suitability and bird density when social dominance is considered by the model (from Fretwell and Lucas, 1970).

(Klopfer and Ganzhorn, 1985). Many factors underlie habitat selection; these factors do not act equally for all species or even for all populations of a single species. Hildén (1965) termed these factors as *proximate* and *ultimate*. Proximate factors are those that, when present in adequate abundance, elicit a settling response by birds to use a certain location. Examples of proximate factors include song perches, nest sites, and the structure and composition of the vegetation. James (1971) termed the composite of all

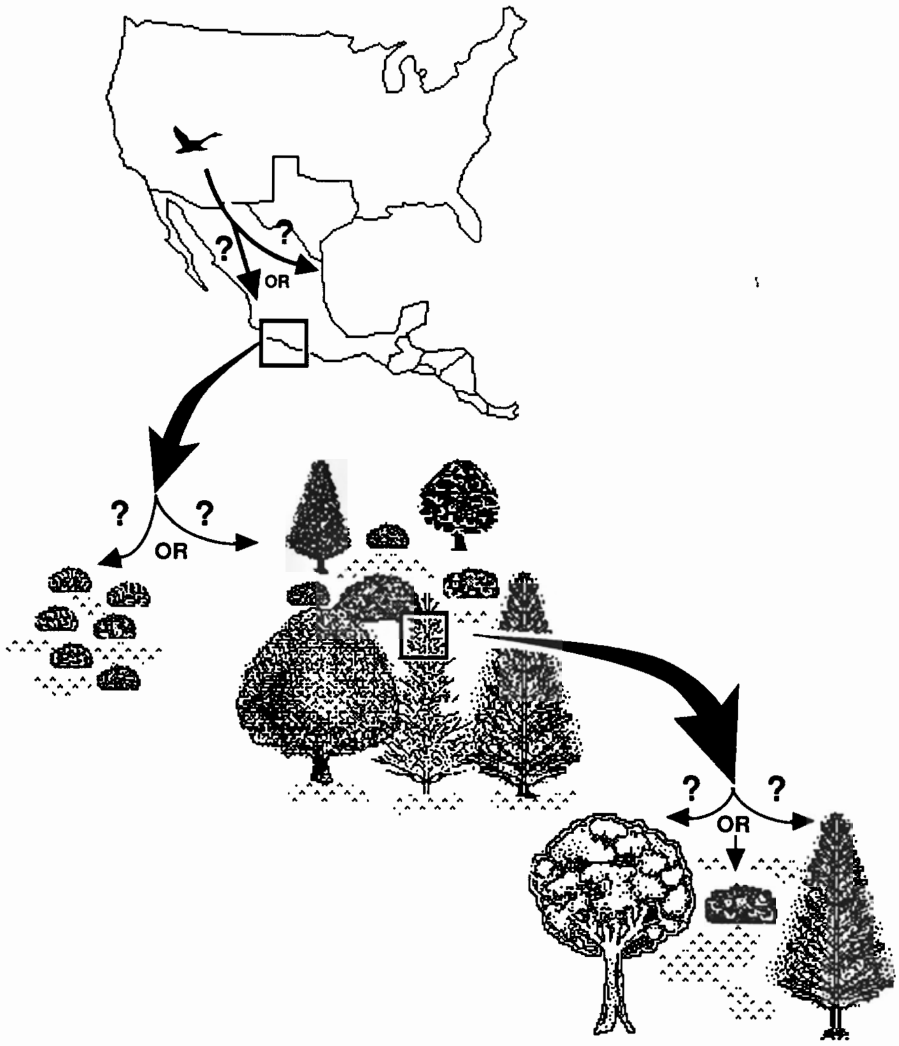

FIGURE 5. Hierarchical decision-making process of habitat selection by migratory birds (from Hutto, 1985).

factors as a species' "niche gestalt." Ultimate factors are considered those tied directly to survival and reproduction of individuals and species. The distinction between proximate and ultimate factors is not always clear. Our point, however, is that conditions must be sufficient for a bird to settle an area; and, once the bird is there, conditions must be adequate for it to survive and ultimately reproduce. This framework for habitat selection is not just restrictive to areas where birds breed. It is also applicable to areas that birds use during winter or migration, for example.

3.1.1. Morphological and Physiological Constraints

The internal and external morphology of birds allows them to exploit a certain subset of possible resources and to use certain habitats (Karr and James, 1975; Ricklefs and Travis, 1980; Miles and Ricklefs, 1984; Winkler, 1988; Block et al., 1991). Bill morphologies are variable in size and shape, each suited to handle different types of foods efficiently. Among seed-eating birds, for example, bill length, depth, and width are strongly correlated with types and sizes of seeds eaten (Lack, 1947; Grant, 1986). Distributions of granivorous species and their habitat-use patterns are strongly influenced by the distributions of plants that produce the seeds. Wing size and shape are also correlated with habitat use (Savile, 1957). Among hawks, for example, accipiters with long tails and short wings are well adapted to fly through forests, whereas buteos with long-broad wings and short, broad tails are better adapted for soaring. Richardson (1942) described a suite of adaptations that facilitate foraging by bark-foraging birds; Dilger (1956) used tarsus length to explain habitat differences among thrushes; and Grinnell (1917) noted that long tails were often common on chaparral birds. Even small differences in the size, shape, and structure of birds' feet can explain differential habitat selection by passerines allowing them to perch on different types and sizes of substrates (Winkler and Leisler, 1985). Thus, a species' morphology must be regarded as a set of adaptations that allow it to exploit a unique part of the environment.

Correlations of morphology and ecology are strongest when considering specific aspects of a birds' ecology as opposed to relating morphology to more general life-history patterns (Block et al., 1991). For example, Ricklefs and Travis (1980) and Miles and Ricklefs (1984) found that foraging behavior was strongly correlated to a species' morphology, whereas Block et al. (1991) recorded only a weak relationship between morphology and general habitat use (Table I). Block et *al.* (1991) concluded that morphology acted as a template of fine-scaled aspects of resource use. Therefore, morphological differences that allowed species to exploit unique microhabitats and more general macrohabitat differences among species act in a complementary fashion to allow species to use unique sets of resources and permit coexistence.

Birds also have specific physiologic adaptations that allow them to efficiently exploit their environment. For example, species of Tetrioninae have well-developed cecae that enable them to digest catkins and buds of plants. Physiologic tolerances to heat and moisture strongly influence habitat use. Apparently, Spotted Owls (Strix occidentalis) seek north-

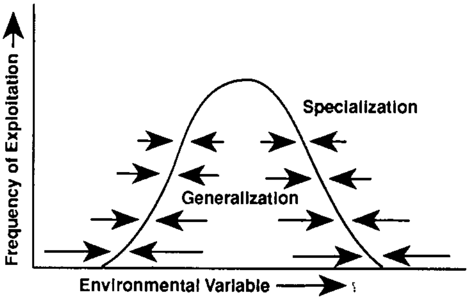

FIGURE 6. Exploitation curve showing interface between interspecific competition promoting specialization and intraspecific competition promotion generalization (from Root, 1967).

American Redstart (*Setophage ruticilla*) when populations of a habitat competitor, the Least Flycatcher (*Empidonax minimus*), declined. Noon (1981a) concluded that the range of habitats used by eastern thrushes increased in the absence of other competing thrushes, although his conclusions have been the subject of debate (Wiens, 1983, 1989a).

Of course, competition is not the only biotic interaction that influences habitat use (Fig. 7). Predators, disease, and parasites can elicit a sufficient functional response to maintain population levels below the threshold at which inter- or intraspecific competition is a factor (Connell, 1975). Predators can also affect movements and habitat use by an animal, rendering otherwise suitable habitat unusable. Other authors (Freeland, 1983; May, 1983; Dobson and May, 1986) have suggested that parasites and disease regulate population numbers and influence species' distribution and habitat use.

Communities can be regarded as complex assemblages of interacting species. Intra- and interspecific relationships are influenced by the structure and composition of vegetation, other complex environmental factors, densities of species, and a myriad of other density-dependent and -independent

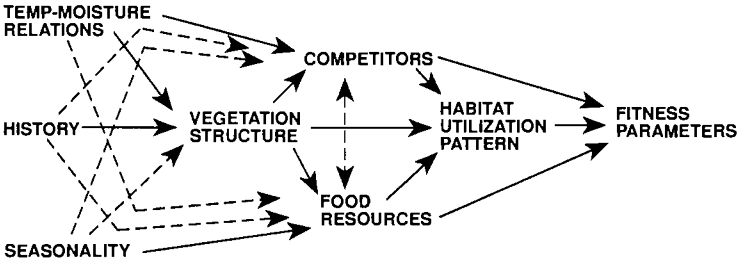

FIGURE 7. Schematic representation of factors and interactions that influence habitat relationships of birds (modified from Karr, 1980).

TABLE I
Percentage of Variation in Habitat Use Explained by Canonical Variates of Morphological Variables, and Percentage of Variation in Morphology Explained by Canonical Variates of Habitat Variables[a]

	Morphological variates		Habitat variates	
Study area	Habitat	Morphology	Habitat	Morphology
All areas	13.9	100.0	61.9	6.9'
Modoc Plateau	13.6	100.0	65.7	8.6
Diamond Mountain	19.0	100.0	65.8	14.6
Kinsey Ridge	16.3	100.0	69.7	7.9
Humbug Creek	13.7	100.0	56.6	6.3

[a] Data from the habitats and morphologies of a guild of ground-foraging birds found in northern California during the 1982 and 1983 breeding season (from Block et *al.*, 1991).

facing slopes and canyons with extensive multicanopied forests to provide thermal relief while these owls roost during hot summer days (Barrows, 1981; Solis and Gutiérrez, 1990). Proper selection of nocturnal roosts by diurnal birds can convey substantial energetic savings, particularly during winter (Stallmaster and Gessaman, 1984; Walsberg, 1985). Other species might seek refuge from rain by using sheltered perches to avoid hypothermia (Walsberg, 1985), and nests are often placed in areas that permit gaseous exchange between the environment and egg, thus influencing development of the embryo. Thus, physiologic tolerances play an important role in defining the limits of the environments used by birds.

3.1.2. Biotic Factors Influencing Habitat Selection

No species exists in the absence of other species. For example, ecologically similar species may preclude potential competitors from using resources either by using the resources first (exploitation competition) or impeding access to resources (interference competition) (Maurer, 1984). Theoretically, differential habitat selection allows closely related species to coexist by minimizing competition over limited resources (Rosenzweig, 1981). Interactions between individuals and species tend to partition available resources. Svardson (1949) and Root (1967) noted that the balance between intra- and interspecific competition plays a large role in determining habitat use by birds as interspecific competition causes species to specialize, whereas intraspecific competition induces species to generalize (Fig. 6). Sherry and Holmes (1988) observed habitat expansion by the factors. Community organization refers to the mechanisms that enable species to partition available resources resulting in the extant community structure (Morrison and Block, in press). These relationships are complex [e.g., food webs (Cohen, 1976)], and it is generally difficult to define cause–effect relationships.

Community organization is rarely, if ever, at a stable equilibrium. Environmental flux is inherent to natural systems, and most species have evolved in response to it. Changes in community structure and organization, even if subtle, can render an area unsuitable for a population in terms of survival or reproduction (Fretwell, 1972). In turn, changes in the population of one species can potentially impact habitats and populations (positively or negatively) of other species, both in the long and short term. Predicting which species will be impacted and how their populations might respond is not always apparent or possible.

Wiens (1989a, 1989b) provided a splendid, state-of-the-art summary and synthesis of avian community ecology. He admonished ornithologists to be skeptical in their assessment and interpretation of causal factors responsible for observed community patterns. Historically, many ornithologists considered interspecific competition, or permutations of this mechanism, such as "the ghost of competition past" (Connell, 1980) to explain observed community patterns. To their credit, Wiens and his co-workers have been successful in pointing out that numerous other mechanistic factors can be responsible for influencing avian habitat use and community structure (Wiens, 1985) (Fig. 8). Wiens summarized these factors in a philosophical context with an 18-point *desiderata* that is as applicable for single-species studies as it is for multiple-species ones (Table II).

Regardless of the exact biotic interactions that influence populations

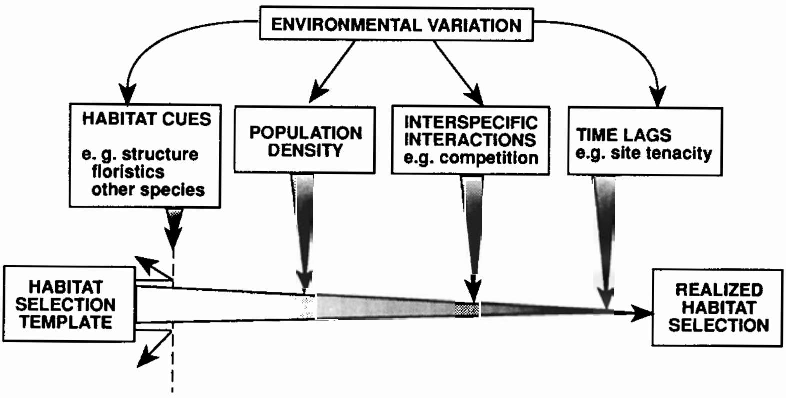

FIGURE 8. Factors influencing habitat selection by birds (from Wiens, 1985).

TABLE II

Recommendations for a More Rigorous Approach to Avian Community Ecology[a]

1. Be explicit about defining the community studied and justify the definition.
2. De-emphasize community macroparameters and focus on individuals, especially aspects relating to energetics, density effects, and habitat selection.
3. Use resource-defined guilds as a framework for intensive comparative studies.
4. Consider both ecological and evolutionary constraints on community patterns.
5. Consider all life stages in community analyses and evaluate the effects of community openness vs. closure.
6. Conduct studies, interpret results, and generalize from them within the appropriate scales in time and space for the biota investigated.
7. Avoid thinking of communities as either equilibrium or nonequilibrium, but examine the dynamics and variability of community measures as features in their own right.
8. Conduct long-term observational and experimental studies.
9. View communities in a landscape context, considering the effects of habitat-mosaic patterns and abandoning notions based on assumptions of spatial heterogeneity.
10. Focus on factors influencing community assembly as a conceptual framework for community studies.
11. Deal with the effects of multiple causes on community patterns.
12. Emphasize the importance of defining and measuring resources and testing the assumption of resource limitation.
13. Develop specific, mechanically based theory.
14. Frame hypotheses in precise, testable terms whenever possible.
15. Take into account the effects of feedback relationships, indirect interactions, time lags, and nonlinear responses.
16. Avoid extrapolating from particular taxa or habitats, and avoid especially a "north-temperate bias" in thinking about communities.
17. Recognize the importance of replication in observational and experimental studies.
18. Do not shun or avoid controversy.

[a] From Wiens, 1989b.

and distributions of species, ornithologists must recognize that these processes can have a substantial role in shaping habitat selection by birds. Equally important is to acknowledge that these ecological processes are complex and dynamic, and cause-and-effect relationships are usually not readily apparent (Wiens, 1989b). However, perturbations to the system that result in a change in numbers of one species or alterations to the habitat will alter patterns of habitat use by other species as well.

3.1.3. Resource Distribution in Time and Space

Actual habitat use is influenced by a number of factors, including the quantity, quality, distribution, and juxtaposition of resources (Wiens, 1986). Any discussion or description of habitat use must consider spatial and temporal patterns over time to incorporate variations in resource abundance and availability (Southwood, 1977). This latter point is quite important because various biotic (e.g., density, competitors, predators) and abiotic (e.g., weather, fire) factors may render otherwise suitable resources unavailable to the animal. Further, habitat use by birds is certainly not static in time or space. Temporal shifts can occur within a season, between seasons, and among years. These temporal shifts are largely influenced by the specific life-history activities and the spatial arrangement of available resources.

Species often require unique resources for different aspects of their life histories. For example, resources that a species requires for nest construction might differ substantially from attributes of the location where the nest is placed (Martin, 1991). In turn, food resources might occur in locations altogether different from nest sites or the location of nest materials. Thus, one must consider the relative placement of these resources that allows individuals to use them effectively.

Types of activities that require specific environmental components include nesting, foraging, roosting, and singing (third-order selection, sensu Johnson, 1980). For example, Collins (1981, 1983) noted differences in song perches and nest sites of eastern warblers, and Williams (1990) identified differences in foraging and nesting sites of Northern Orioles (Icterus galbula) in central coastal California.

Seasonal changes often correspond to different life-history requirements and also different migratory strategies of birds. Requirements can differ by stages within a season, for example, during nesting and fledging periods, or between seasons, such as breeding and nonbreeding. Seasonal differences in habitat use can range from shifts in tree-species use by resident species to use of drastically different areas by migrant birds (Conner, 1981; Hutto, 1985; Morrison et al., 1985; Terborgh, 1989; Block, 1991). Migratory birds typically use different habitats on their breeding and wintering grounds, and possibly different habitats during migration. Hutto (1985) observed that migrant birds used different environments during breeding, migration, and winter. He concluded that breeding birds were constrained by nesting requirements, whereas habitat use by migrating or wintering birds were more strongly influenced by the abundance and distribution of food resources. A similar pattern is demonstrated by nomadic species, such as the Short-eared Owl (Asio *flammeus*) or the Lewis's Woodpecker (Melanerpes lewis), which may use different habitats, depending on prey availability (Bock, 1970; Clark, 1975).

Year-to-year differences in habitat use often reflect the distribution of available resources, as modified by biotic and abiotic factors. Wiens (1977) asserted that patterns perceived under restricted environmental conditions might be misleading with regard to understanding the factors that regulate the populations of species. For example, habitat use by a population during periods of scarce resources would differ drastically from that during periods when resources were plentiful. A short-term study conducted during either of these extremes might reach conflicting conclusions regarding habitat use. Thus, it is critical that analyses of habitat use be described within the temporal context of the data. Certainly, long-term data are required to understand habitat use under a continuum of environmental conditions.

3.1.4. Vegetative Structure and Composition

Vegetative structure is frequently assumed to be the primary proximate factor determining where and how species use resources. Structure can refer to the layering of the canopy or the horizontal dispersion of patches. Vertical vegetative structure has often been cited as a primary determinant of species diversity (MacArthur and MacArthur, 1961; Recher, 1969). The hypothesis derived from these studies was that the number of potential niches increased with increasing vegetative diversity. Tomoff (1974) and Willson (1974) suggested that patchiness also influenced species diversity.

Rotenberry (1985) evaluated the influence of vegetative structure and floristics as determinants of habitat use by birds. He found that plant species composition strongly influenced the distribution of shrub-steppe birds. Additionally, MacNally (1990) suggested that floristic habitat relationships of birds are often influenced by the scale of observation. He stressed the importance of considering different observational scales to determine the relative significance of structural and floristic attributes of the habitat.

The relationship between birds and specific plant species is certainly not new. For example, Sage Grouse (Centrocercus urophasianus) is strongly associated with sagebrush (Artemesia tridentata), Chukar (Alectoris chukar) is associated with cheatgrass (Bromus tectorum), and Chestnut-backed Chickadees (*Parus rufescens*) appear to follow the distribution of Douglas-fir (Pseudotsuga menziesii) in California (Brennan and Morrison, 1991). More intensive study into floristic determinants of habitat selection by additional species will likely reveal similar patterns. Thus, it is clear that both vegetation structure and floristics are important factors in habitat selection by birds and should be included in all studies of bird–habitat relationships.

3.1.5. Birds as Environmental Modifiers

As Southwood (1977) noted, the activities of organisms can have pronounced influence on altering their environment. Foraging by birds for example, can regulate the abundance and distribution of seeds and insects, and affect the vigor of trees. Many species of birds are adapted to forage at different locations in the forest and at different locations in a tree, use different foraging methods, and feed on different distributions of prey (Richardson, 1942; Lack, 1947; Winkler and Liesler, 1985). For example, many warblers and vireos are foliage-gleaning insectivorous birds; thrushes often consume berries and drupes when ripe; and woodpeckers glean insects from bark or excavate prey buried within the furrows or underneath bark. Few birds, if any, specialize on one type of prey but rather consume a wide variety of food types (Otvos,1979). Thus, it is probably less important to consider the effect of any one species of birds on the distribution and abundance of foods than it is to examine the effects of all birds simultaneously.

Although birds probably cannot exert an adequate functional response to depress the population of an insect once it reaches epidemic numbers, many researchers think that birds help to maintain insects at low numbers between outbreaks (Otvos, 1979; Crawford and Jennings, 1989; Holmes, 1990). Other studies have shown that birds can significantly reduce the abundance of some arthropods in nonoutbreak years (Holmes et al., 1979); Fowler et al., 1991). Epidemics of insects, however, are considered more a symptom of poor environmental conditions than a widespread occurrence of all forest stands (Mattson and Addy, 1975). Poor conditions render a site more vulnerable to insect outbreaks when triggered by some environmental event, such as weather or fire. During such conditions, populations of insects can increase at a rate that exceeds the ability of birds to regulate them. On other sites, however, birds control insect populations directly by preying upon them, and indirectly by influencing populations of insect parasites, predators, and pathogens (Otvos, 1979).

Birds also act as dispersers of seeds. For example, Scrub Jays (*Aphelocoma coerulescens*) collect oak (Quercus spp.) acorns and cache them at various locations (Grinnell, 1936; Grinnell and Storer, 1924). Often caches go unused and the buried acorns germinate and grow at locations far from their parent tree. Western Bluebirds (Sialia mexicana) and other thrushes eat the ripened fruits of various trees and shrubs during fall and winter. Seeds of these fruits are not digested, and are later egested. These egested seeds often grow to mature plants. Thus, birds that consume seeds or fruits can distribute seeds to locations far from the source shrub or tree. This dispersal ability can influence the distribution and, hence, structure and composition of plant communities across the landscape.

Other roles birds play in forested ecosystems are to disperse ephiphytes (Reid, 1991) and facilitate the spread of pathogens (Otvos, 1979). The Western Bluebird consumes the fruit of mistletoe and egests the seeds elsewhere, promoting the spread of this epiphyte to other trees. Reid (1991) speculated that there may be widespread coevolutionary relationships between birds and mistletoe at different locations in the world. Excavations by woodpeckers may render trees more susceptible to infestations by pathogens or fungi. Foraging and nest construction by woodpeckers in dead or decaying wood also accelerate decomposition of the tree and facilitate nutrient cycling (Otvos, 1979).

Hence, the role of birds in the environment must be regarded as mutualistic. The components of the environment provide the necessary conditions for birds to survive and ultimately breed, and bird activities directly and indirectly aid in maintaining or modifying certain aspects of their habitat.

3.2. Is the Habitat Concept a Unifying Theory in Ornithology?

We have alluded to this question earlier in several parts of this chapter. Although this question is rhetorical, the previous historical and theoretical examples clearly show that the habitat concept is firmly based in ornithology. Furthermore, ornithologists have been among the leaders in developing specific aspects of the habitat concept that have been applied throughout the entire field of vertebrate biology. In a general sense, the habitat concept is used to describe where birds and other animals are found and how biotic and abiotic factors of the environment influence their distribution and abundance. More specifically, the habitat concept is deeply entrenched in explanations of the factors, patterns, and processes that underlie the evolutionary history and potential and, hence, fitness of birds at the individual, population, and community levels.

In summary, to answer the question posed at the beginning of this section, we contend that the habitat concept is one of the few unifying theories in contemporary ecology and especially ornithology. This is clearly shown by connections between habitat and natural selection drawn by Southwood's (1977) templet model, and the numerous other specific empirical examples summarized above. If ornithologists are to be successful in applying the habitat concept to solving problems that face many avian populations and species, it is essential to understand the theoretical notion of habitat as a basic, unifying concept.

4. APPLICATIONS OF THE HABITAT CONCEPT

4.1. Influence of Scale on Avian Habitat Analyses

Interpretations of habitat studies are a function of the scale at which the research was conducted (Wiens, 1985, 1989a, 1989b; Brennan et *al.*, 1987; MacNally, 1990; Block and Morrison, 1991). A study conducted at one location and during one time might apply only to that place and time of study. Furthermore, different patterns emerge when one examines habitat-use patterns at different scales (Wiens et *al.*, 1986, 1987; MacNally, 1990; Block et *al.*, 1991).

Researchers should not ignore historic events responsible for present distributions. That is, one must consider habitat use in the context of geologic events that structured an area. This knowledge is critical to understanding how anthropogenic modifications to natural ecosystems have influenced distributions and the quantity and characteristics of environments used by birds. Thus, considerations of evolutionary, biogeographic patterns are especially important to explain extant distributions and habitat associations of birds (Mengel, 1964; Selander, 1965; Hubbard, 1973; Gutiérrez et *al.*, 1983).

From the standpoint of spatial scale, avian habitat relationships can be considered from detailed microhabitat approaches to examining broad continental or global patterns. Johnson's (1980) hierarchical approach is particularly relevant here. Habitat analyses can be conducted along a continuum from his first-order selection (geographic range of the species) to fourth-order selection (actual procurement of a resource from a site). Because the scale of observation will strongly influence the resolution of habitat use, multiple scales should be considered in any study. The exact choice of levels depends on specific study objectives, but we argue that at the very least habitat use should always be considered at both macrohabitat [Johnson's (1980) second-order] and microhabitat [Johnson's (1980) third-order] levels.

Detailed examinations of features within territories (third-order) or stands emphasize fine-grained aspects of habitats: leaf structure, vegetative structure and composition, prey distribution, microclimate, etc. As the scale of observation increases (second-order), research focuses less on these fine- grained aspects of habitats, but considers general distributional patterns along macrohabitat gradients. The recent emphasis of landscape ecology and the associated technology of geographic information systems (GIS) provides avian ecologists with novel ways to examine these macrohabitat gradients across expansive geographic areas. The influences of landscape patterns—such as the size, shape, interspersion, and juxtaposition of major cover types—can be examined to evaluate their role on bird-habitat use. This avenue of research will provide a key link to explain distributions of birds.

Temporal scale is also important because birds do different things to meet varying functional needs during different times of the year and they also exhibit habitat shifts between years. Seasonal shifts in habitat use can be drastic, as in the case of migratory birds, or subtle, as with resident species. This is particularly true for neotropical migrant birds that generally use different habitats on breeding, migratory, and wintering grounds (Hutto, 1985; Terborgh, 1989; Hagan and Johnston, 1991). Even resident, generalist birds such as chickadees shift their habitat-use patterns in relation to seasonal cycles (Brennan and Morrison, 1990). Most birds also exhibit habitat shifts between years. These shifts can result from numerous factors such as weather, food abundance, and densities of conspecifics, competitors, and predators. Regardless of the underlying reason, it is critical to recognize that habitat-use patterns viewed in one year may be unique to that particular year. Thus, accurate descriptions of habitat use are generally possible only through long-term studies. Long-term studies are needed to understand the influences of slow processes, rare or episodic events, highly variable processes, and complex phenomena on habitat use (Franklin, 1989). As Wiens (1977) noted, most research views these events and processes through a very restricted window that often fails to describe adequately the big picture. Unfortunately, no clear guidelines exist to define the length of time for long-term studies. Strayer et *al.* (1986) provided two somewhat contrasting guidelines for defining "long-term." The first suggested that a long-term study would continue for the length of the generation time of the study organism. The second guideline is that the study should continue for a longer time than for similar studies conducted previously. Obviously, the first definition has a biological basis, whereas the other is based on human expediency, which may have little relevance to biology. Future research is needed to more clearly define what actually constitutes a long-term study.

4.2. Designing Avian-Habitat Studies

Various designs are used in studies of bird–habitat relationships. Certainly, the exact design used depends entirely on the study objectives. Green (1979) outlined ten principles for designing and implementing environmental studies (Table III). Although these ten principles clearly apply to any investigation of avian habitat use, they are rarely followed by ornithologists. We acknowledge that logistical considerations often preclude implementation of all ten principles, but ornithologists must consider the ramifications of ignoring them on results of their research. Too frequently, ornithologists take the "shotgun approach" by collecting as much information as their time and budgets allow and then parlaying those data into one or more publications. Although this approach has yielded useful information in the past, we argue that adherence to or, at the very least, consideration of Green's (1979) and Wien's (1989b) (Table II) principles will result in stronger, more reliable research results.

Green's (1979) first principle requires the investigator to state a *priori* the questions to be addressed by the research. The form of the question will

TABLE III
Ten Basic Principles to be Used in Designing and Conducting Bird-Habitat Studies[a]

1. Be able to state concisely to someone else what question you are asking.
2. Take replicate samples within each combination of time, location, and any other controlled variable.
3. Take an equal number of randomly allocated replicate samples for each combination of controlled variables.
4. To test whether a condition has an effect, collect samples both where the condition is present and where it is absent.
5. Carry out some preliminary sampling to provide a basis for evaluations of sampling design and statistical analysis options.
6. Verify that your sampling technique is sampling the population that you think you are sampling, and with equal efficiency over the entire range of conditions encountered.
7. If the area to be sampled has a large-scale environmental pattern, break the area up into relatively homogeneous subareas and allocate samples to the proportion of each subarea.
8. Verify that your sample unit size is appropriate for the size, densities, and spatial distributions of the organisms you are sampling. Then estimate the number of replicate samples required to obtain the desired precision.
9. Test your data to determine whether the error variation is homogeneous, normally distributed, and independent of the mean. If it is not, then either transform the data, use a nonparametric procedure, or use an appropriate sequential sampling design, or test against a simulated null hypothesis data set.
10. Having chosen the best statistical test for your data, stick with the result. An unexpected or undesired result is not a valid reason for rejecting a method of analysis and hunting for a better one.

[a] From Green. 1979

depend on the type of research being done. If the research is descriptive, these questions can be stated in the form of specific study objectives. Conversely, if the research is experimental, the question should be stated as a null hypothesis with alternative hypotheses also stated. The next two principles restate the need for randomization and replication. These concepts underlie all scientific research, but are ignored frequently. Most parametric and nonparametric statistical methods assume that samples are obtained randomly. Cochran (1977) presents different sampling methods (e.g., simple random, stratified-random, cluster, two-stage cluster) commonly used in scientific investigations and provides proofs to demonstrate that they provide unbiased estimates of most statistical parameters. Failure to collect random samples may result in biased results that reflect preconceived notions of the investigator. Replication is necessary to determine if perceived relationships are indeed patterns or simply unique to place and time of study. Often researchers are guilty of pseudoreplication (sensu Hurlbert, 1984) by collecting many samples from a restricted universe and then extrapolating their results elsewhere. Their results typically apply only to the place and time of their study. The use of controls, the fourth principal, is particularly important to experiments. Controls allow the investigator to separate deterministic change as the result of a specific treatment from stochastic environmental fluctuations. Principles five through eight restate the need for pilot studies to test and verify that a planned methodology is adequate to meet study objectives or to test the stated null hypotheses. Investigators rarely conduct such pilot studies, and often must restate their objectives after data collection is complete because their study design did not address the initial study objectives. As Green (1979:31) notes "Those who skip this step because they do not have enough time usually end up losing time."

4.2.1. Correlative, Focal-Bird, and Experimental Approaches

As we noted above, ornithologists use a multitude of designs in avian-habitat studies. Three basic study designs used to relate birds to habitat characteristics are (1)correlative approaches relating bird abundances to habitat characteristics; (2) focal-bird approaches where habitat characteristics are measured at the location where a bird was observed; and (3)experimental approaches to observe effects of environmental change on habitat use (Larson and Bock, 1986; Brennan et *al.,* 1986, 1987). Correlative approaches entail relating bird abundances to a set of habitat characteristics measured at the general location of where abundances were estimated. Unfortunately, correlative approaches generally rely on multiple-linear regression and often explain only a minor amount of the variation in habitat use (e.g., Maurer, 1986; Morrison et *al.,* 1987). The failure of these approaches to provide useful habitat descriptions is partly because accurate measures of bird abundances are difficult to obtain and partly because of difficulties with choosing and measuring habitat variables correctly (Capen, 1981; Verner, 1985). In contrast, focal-bird plots often provide better descriptions of bird habitats than correlations of habitat to bird abundances (Larson and Bock, 1986). Further, focal-bird approaches offer flexibility in analyses of the data and can be applied both to autecological and synecological studies. An autecological study might contrast focal-bird plots with a set of random plots to evaluate whether and how a species uses the environment nonrandomly. Analyses can be done univariately, but perhaps hold greater potential when done multivariately (Martinka, 1972; Brennan et *al.,* 1987). Focal-bird plots could be used in synecological studies to order species along environmental gradients using a variety of multivariate ordination techniques (e.g., James and McCullough, 1990). The primary limitation of the focal-bird approach is that habitat use cannot be related to population densities. This limitation, however, may not be too critical because density alone is not the appropriate measure of habitat quality (Van Horne, 1983). Focal-bird approaches are nevertheless amenable to estimating other population parameters such as reproduction and survival if the study design includes nest monitoring or following the fate of marked birds.

The most rigorous approach to investigations of avian habitat relationships is the use of experiments. Experiments can be performed in the laboratory or in the field. For example, Klopfer (1963) used laboratory experiments to determine foliage preference by Chipping Sparrows (*Spizella* passerina). Field experiments, however, are extremely difficult to implement because of the costs involved and also because of the inability to control for the plethora of extraneous sources of variation. Because environmental conditions vary widely in time and space, numerous replicates are needed to sort the influences of such variations on habitat use from the effect of the treatment or specific factor under study. Often field manipulations applied to just one area are cost-prohibitive and, if applied to multiple replicate sites, the costs become astronomical. James and McCullough (1990)suggested that such costs can be ameliorated if research is coordinated with planned land-management activities. Such an approach may be worth pursuing, but also entails a vast amount of cooperation and communication between research and management to ensure that a rigorous design can be implemented successfully. Regardless, we think that researchers must move from correlative approaches to the application of experiments to advance the knowledge of bird–habitat relationships.

4.2.2. Radio Telemetry

The rapidly advancing technology of radio telemetry is providing opportunities to examine bird–habitat use in novel ways. For example, miniaturization in circuitry and power supply has reduced the size and increased the duration of telemetry transmitters. Results from telemetry studies have provided tremendous insight into habitat use and movement patterns of Brown-headed Cowbirds (Molothrus ater) (Rothstein et al., 1984), Montezuma Quail (Cyrtonix montezumae) (Stromberg, 1990), California Quail (*Callipepla californica*) (Kilbride et al., 1992), Northern Orioles (Williams, 1990), Spotted Owls (Solis and Gutierrez, 1990), and numerous other species. Radio telemetry allows investigators to record habitat use without actually seeing or hearing the birds. Further, investigators can follow birds continuously, recording the sequence in what habitat components the birds use and how. This type of study design is particularly suitable to analysis by the use of Markov chains (Raphael, 1990) to determine the probabilities of use of different patches. However, a key limitation of most telemetry studies is that cost and logistical constraints limit the number of individuals that can be followed. Without considerable financial resources and a small army of technicians, it is usually impossible to use telemetry to generate broad-scale data sets on a particular species. Thus, most investigators who use radio telemetry are limited to relatively small geographic scales of investigation with a limited number of individuals.

Telemetry data are not without inherent biases. Perhaps the primary bias is the mislocation of animals (Nams, 1989; Samuel and Kenow, 1992). Failure to locate animals accurately can result in misinterpretations of habitat use. Accurate locations are particularly difficult in areag where vegetation is arrayed in small heterogeneous patches and where topography (e.g., mountainous terrain) adds confusion to the direction from which signals are transmitted. A critical aspect of any telemetry study is to field check the accuracy of location fixes. This can be done by triangulating the location of known radio locations throughout a study area and then using post-hoc procedures to adjust the triangulations. White and Garrott (1986) and Samuel and Kenow (1992) provide techniques on how to minimize telemetry error to obtain greater accuracy of habitat use.

Besides sample-size limitations and telemetry error, transmitters may influence behavior, survival, and reproduction. For example, Hogge (1991) found that behaviors of Acorn Woodpeckers (Melanerpes formicivorous) with transmitters differed significantly from those without transmitters. Presently, Spotted Owl researchers are debating over whether transmitters do (Paton et al., 1991) or do not (Foster et al., 1992) affect survivorship. Both of these groups of researchers agree, however, that radio transmitters affected reproduction of the owl. Others have noted that transmitters can affect a bird's flight and agility (Pennycuick and Fuller, 1987), susceptibility to predation (Marks and Marks, 1987), and metabolism (Gessaman and Nagy, 1988). Thus, researchers should be aware of all of these potential biases when designing and interpreting the results of radio-telemetry studies.

4.2.3. Influence of Sampling Techniques and Sample Size

Sampling techniques and sample size have a direct bearing on inferences made from studies of avian habitat relationships. The selection of sampling methodology made at the outset of a study will clearly influence interpretations of the results. James and Shugart (1970) presented a methodology for measuring habitat characteristics that was later refined by Noon (1981b). Although a standard methodology is meritous, different situations require different methods to be employed. Mueller-Dombois and Ellenberg (1974) and Cook and Stubbendieck (1986) provide guidance on established methods to measure vegetation in most situations. Unfortunately, some variables deemed important to birds by ornithologists such as canopy structure have no established way to be measured, leaving the specific techniques used up to the ingenuity of the researcher. Likely, the exact variables to be measured will vary with the scope and scale of the research. With terrestrial birds, selected aspects of vegetation, such as tree density, crown closure, understory and vertical structure, are almost always measured. From the standpoint of avian habitat analyses, vegetation measures typically fall into two broad categories: (1) physical structure, and (2) floristic composition. A sound analysis of avian habitat relationships requires that both of these categories be addressed (Rotenberry, 1985). Physical and chemical factors also must be considered in virtually any habitat analysis. For example, directional aspect of nest cavity or roost site selection often influences habitat occupancy (Bergin, 1991). In estuarine and marine environments, salinity and sediment gradients can have great influence on distribution and abundance of sandpipers (Kelsey and Hassall, 1989) and eider ducks (Nystrom and Pehrsson, 1988). Vegetation is almost always profoundly influenced by the types of soil present on an area. Thus, information on soil types can often be of great value in analyses of avian habitat use. For example, Ormerod et *al.* (1991) found that Dipper (Cinclus cinclus) clutch size and body mass were inversely related to soil acidity.

Whereas we do not advocate a standard, universal methodology for measuring habitat, we assert that three considerations are crucial to any sampling design to quantify habitat characteristics. First, measurements must be accurate; that is, they must quantify characteristics as they occur in the field with minimal measurement error. Second, measurements must be precise and repeatable among independent observers. And third, adequate independent samples must be obtained for precise estimates of the variables.

Block et *al.* (1987) compared ocular estimates of habitat variables with results obtained from established mensural tools (e.g., diameter tape, clinometer, measuring tape) and methods (e.g., line intercept). Three observers visually estimated habitat characteristics on the same 75 plots, and then used tools to measure the same variables. They found that at least one observer differed significantly from the others in ocular estimates of most variables considered. When estimates of each observer were compared with the measured values, significant differences were found for most variables. Unfortunately, observers differed from the measurements in different directions; that is, when one observer significantly overestimated a variable, another significantly underestimated the same variable. These results are certainly disturbing because a large number of avian habitat studies have used ocular estimates to quantify habitat structure. The accuracy of these results are unknown and perhaps questionable. Because ocular estimates are commonly used in ornithology and provide the basis for what we know of the habitat relationships of many species, we may know far less about habitat requirements of species than we allow ourselves to believe.

Sample size and the reliability of information are factors that rarely seem to be addressed in the methods sections of scientific papers on avian habitat relationships (Morrison, 1988). Typically, researchers collect as many samples as is possible or convenient and use the data for descriptive purposes, tests of null hypotheses, or both. Rarely, however, do investigators justify the sample sizes used in their analyses (Brennan and Morrison, 1990). Block et al., (1987) used a modified bootstrap (Efron, 1982) analysis to estimate the number of sample plots needed for precise estimates of selected habitat variables (Fig. 9). When variables were measured, from 35 to 50 plots were needed. Conversely, Block et *al.* (1987) could never determine the number of plots needed for precise estimates of most variables when ocular estimates were used. Thus, not only are ocular estimates probably inaccurate, they are imprecise as well.

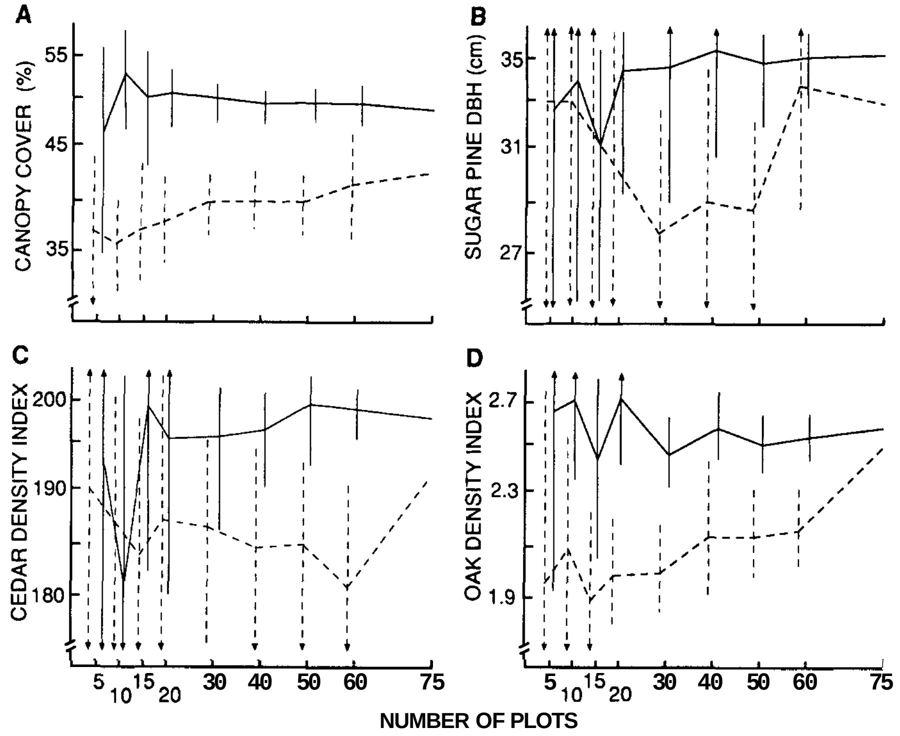

FIGURE 9. Dynamics of number of samples on precision of ocular estimates (dashed horizontal lines) and measurements (solid horizontal lines) of bird habitat characteristics. Vertical lines represent 1 standard deviation from mean (from Block et al., 1987).

Sample size and the power of statistical tests go hand in hand. Two types of errors are possible in tests of null hypotheses: type I error, which is to mistakenly reject the null hypothesis; and type II error, which is to fail to reject a false null hypothesis. The power of a statistical test is the probability of not committing a type II error (Toft and Shea, 1983). Three factors can effect statistical power: the critical level of alpha, the sample size, and the effect size. The smaller the alpha selected for avoiding a type I error, the greater the probability for a type II error and the lower the power of the test. Larger sample sizes provide more reliable estimates of the parameter of interest and reduce the probabilities of both type I and type II errors. Effect size refers to the magnitude of the effect that an investigator desires to test. The larger the critical effect size, the easier it is to detect differences, and the greater the power of the given test. Thus, researchers should consider the influence of these three factors on the power of their analyses and ability to detect differences when they do indeed occur.

In summary, we implore researchers who work in the arena of avian habitat ecology to evaluate their methods carefully. A basic premise of research is that methods are repeatable by independent observers. Subjective methods such as ocular estimates (i.e., guessing) do not meet this premise because of vast interobserver differences. Plant and range ecologists have established systematic, repeatable methods to quantify most vegetative characteristics imaginable (Mueller-Dombois and Ellensberg, 1974; Bonham, 1989; Cook and Stubbendieck, 1986). Ornithologists would be well served to use these methods when appropriate. Further, ornithologists must acknowledge the need to collect adequate numbers of samples. Morrison (1988) and Brennan and Morrison (1990) outlined one technique to determine sample size, and Petit et al. (1990) provided another. Most general statistics books provide established formulas to calculate the number of samples needed to meet predetermined levels of accuracy and precision. As Morrison (1988) noted, ornithologists must justify the number of samples collected both from logistical and statistical perspectives. Failure to do so may render their research invalid.

4.2.4. Heterogeneity in Sex and Age

Age and sex of individual birds are potentially confounding factors that must be addressed in studies of avian habitat. Grubb and Woodrey (1990) reviewed sexual differences in the use of foraging substrates by woodpeckers of the genus Picoides. Aulen and Lunberg (1991) found that male White-backed Woodpeckers (Dendrocopus leucotus) used live trees for foraging more frequently than females. Morton (1990) observed male and female Hooded Warblers (Wilsonia citrina) using completely different habitats on the wintering grounds, with males generally using forest and females using shrub or field habitats. Conversely, Jarvinen (1986) observed that male and female Redstarts (Phoenicurus phoenicurus) in Finnish Lapland had near complete overlap in foraging patterns, and attributed it to a structurally simple and impoverished habitat.

Age is also known to play a significant role in reproduction, survival, and foraging success of birds. Typically, adult birds are more efficient and successful than young birds at obtaining food. The literature on wading and diving birds provides a large number of examples (see for example, Lack, 1966; Orians, 1969; Recher and Recher, 1969; Dunn, 1972; Morrisop et al., 1978).

When possible, habitat studies should first test for heterogeneity among individuals and age classes, and between sexes. Comparisons of habitat use among individuals requires that all birds within a population be banded, which is certainly an arduous, if not impossible, task. For dichromatic or obviously dimorphic species, intersexual comparisons are possible without banding (Hanowski and Neimi, 1990). Researchers should be aware that pooling data across individuals, sexes, and ages runs the risk of misleading results if habitat heterogeneity exists. Pooling across ages or sexes when heterogeneity exists may provide average results that represent neither class. Thus, only if individual, sexual, or age differences do not exist, are investigators justified in pooling data.

4.3. Quantitative Analysis of Avian Habitat Relationships

The two general ways that ornithologists attempt quantitative habitat analyses are by descriptions and predictions. Ornithologists have progressed further within the descriptive than the predictive arena. Quantitative descriptions of avian habitat relationships were an outgrowth of the qualitative natural history era. Amazingly, these qualitative descriptions have stood the test of time when compared with large contemporary data sets. For example, Grinnell's (1904) habitat descriptions of Chestnut-backed Chickadees were supported by the extensive data set presented by Brennan (1989). Species accounts provided by Grinnell and Miller (1944), Gabrielson and Jewett (1940), Phillips et *al.* (1964), and many others still provide the best existing knowledge for most species. The need for more detailed knowledge, both to satisfy the human need to understand their surroundings and also to understand the effects of anthropogenic change on the earth's biota, has necessitated the development of sophisticated, novel techniques to describe avian habitats.

Relating direct observations of individual birds to predetermined habitat parameters is by far the most common method used in contemporary quantitative habitat analyses. Typically, an observer detects birds along fixed or random transects, marks and plots their location, and measures a series of variables. Depending on the particular species or group of birds, any number of different variables may be appropriate for an analysis of habitat relationships.

These analyses can be done at different spatial scales and to meet different objectives (e.g., Johnson, 1980). For example, general macrohabitat descriptions are provided by relating the presence of birds to general vegetation types or seral stages of vegetation types. More fine-scaled information is possible on characteristics within that vegetation type, such as the size, density, dispersion of trees, structural features, and floristic composition. These analyses can be presented in various ways. One approach is simply to describe the habitat characteristics of where the species was found. Alternative ways are to compare these values with values from areas where the animal was not found or from random sites to identify features that distinguish the bird's habitat from surrounding, similar areas.

These approaches are useful, but the latter two should not be done without the former. Because features of the habitat do not differ from the surrounding area, it does not mean they are not important components of a bird's habitat. Documenting how a bird's habitat differs from surrounding areas provides greater detail of characteristics unique to that species' habitat.

4.3.1. Multivariate Statistics

If the objective is to identify the suite of features potentially related to or influencing a species' presence or abundance, then multivariate techniques are indeed practical (Green,1978). Intuitively, multivariate analysis is appealing because it is consistent with Hutchinson's n-dimensional niche concept and incorporates multidimensional aspects of species' habitats. Analyzing habitat components by using univariate statistics is perhaps far less "realistic" than analyzing an array of variables simultaneously. Consequently, the correct application of multivariate statistics has advanced avian habitat descriptions because they allowed ornithologists to describe habitats as a complex array of many different components.

Initially, multivariate statistics were used to describe habitats. Cody (1968) and James (1971) were among the first ornithologists to use multivariate analyses to order species according to their habitat affinities along environmental gradients. Martinka (1972) was one of the first to use multivariate statistics to describe the habitat of a single species in his study of the Blue Grouse (Dendragopus obscurus).

The broad and positive reception of the proceedings from the first symposium on multivariate analyses of habitat relationships (Capen, 1981) attests to the wide application by ecologists of multivariate analyses for describing and predicting habitat relationships. The symposium proceedings edited by Capen (1981) and the prominent role that predictive habitat models were given in the Habitat Evaluation Procedure (HEP) developed by the U.S. Fish and Wildlife Service (USFWS, 1980a,b, 1981) spurred a tremendous amount of multivariate statistical research effort by avian habitat ecologists. A great deal of this work was summarized in the 60 chapters published in the proceedings of the Wildlife 2000 symposium (Verner et *al.*, 1986) evaluating habitat relationships of terrestrial vertebrates. Again, avian examples figured prominently throughout the Wildlife 2000 proceedings. However, the general tone of the Wildlife 2000 proceedings, although generally optimistic about the value and potential of statistical habitat models (especially multivariate ones), contained a considerable number of caveats. There was even a major section titled "When habitats fail as predictors." To the person reading Wildlife 2000, it is obvious that it is a relatively simple matter to develop a habitat model. Unfortunately, it is also clear that testing the accuracy of predictions from a multivariate model is a difficult, time consuming, and costly process that has mostly been neglected by habitat ecologists. One problem is that many so-called models used in HEP were simply "made up" with a ruler and graph paper using qualitative accounts published from the natural history era. Using data-based techniques for developing avian habitat models has been largely neglected, even though it appears to offer an objective strategy for developing and testing avian habitat models and the assumptions on which they are based (Brennan et al., 1986). However, data-based models appear to have promise. For example, Brennan (1991b) found that a Mountain Quail (Oreortyx pictus) habitat model developed with a large data set from northern California (Fig. 10) provided correct predictions in 15 out of 16 instances when independently tested in a different part of this bird's geographic range.

4.3.2. Merits and Limitations of Multivariate Analyses

Initially, multivariate statistical techniques were perceived as a panacea for unraveling some of the complex relationships between birds and their habitats that were hypothesized by earlier workers, such as Grinnell, Stoddard, Leopold, and their contemporaries. These quantitative techniques were perceived as something of a scientific "free lunch" because they added an apparent new rigor to a field of science that had been dominated by qualitative description and prediction. During the 1970s, habitat ecology appeared to be on the cusp of being as quantitative and deterministic as the "hard" sciences, such as physics and chemistry.

In a recent, highly critical review, James and McCullough (1990) identified numerous ways that multivariate statistics have been used and

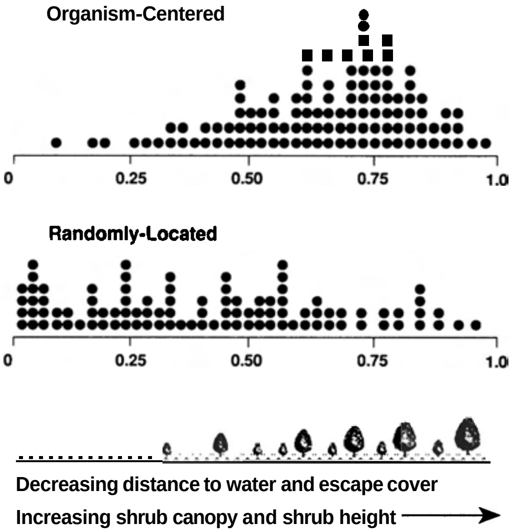

FIGURE 10. Data-based model using logistic regression developed for Mountain Quail (from Brennan et *al.*, 1987).

abused in ecology. Their main conclusion is that although multivariate techniques are necessary for assessing "joint relationships among variables," they are not "a panacea for data analysts" and because of a history of "cavalier applications and interpretations" represent something of a Pandora's box. Rexstad et *al.* (1988) also offered a very critical view of multivariate statistics. They conducted principal components, canonical correlation, and discriminant analyses on a set of unrelated variables that resulted in seemingly significant relationships. They concluded that multivariate statistics could be used to show relationships where they did not, in fact, exist. Whereas Rexstad et *al.*'s (1988) results were certainly intriguing, they were not a realistic test of multivariate analyses and we view their results with some skepticism. We agree, however, with both James and McCullough (1990) and Rexstad et *al.* (1988) that there is no substitute for carefully analyzing multivariate data sets and avoiding unjustified inference.

Ornithologists have numerous opportunities to increase the rigor and appropriateness with which multivariate techniques and models are applied to the study of birds and their habitats. With forest birds, for example, there are numerous opportunities to coordinate field work plans with harvest schedules to test the accuracy of previously developed multivariate models experimentally. James and McCullough (1990) point out that a quasi-experimental approach using paired comparisons can often be of value when an experiment is not feasible. Although time series have been applied to certain ecological situations (Shugart, 1978), this family of techniques has been totally neglected by ornithologists for analyses that describe and predict habitat use by birds through time and space. Application of the response-surface methodology with time series (see Turchin and Taylor, 1992) may be a particularly fruitful avenue of research to pursue for analysis of complex population, foraging, and habitat use data sets.

There is, however, an Achilles heel in the apparent quantitative panacea offered by multivariate analyses. No matter how complex and sophisticated a statistical analysis of avian habitat relationships might be, the bottom line is that without an experimental context, the analyses are correlative in nature. Therefore, a particular analysis might or might not address the causative factors responsible for the emergent patterns of a study. Even with this fundamental limitation, correlative approaches to habitat analyses can often provide great insight into apparent patterns of habitat use in both autecological and synecological contexts. Identifying these types of patterns is the primary step in the development of testable hypotheses of the factors responsible for those patterns (Kolasa, 1989; Tilman, 1989).

4.3.3. Use versus Availability Analyses

A commonly used approach to studies of habitats is to compare areas actually used to those potentially available to a species. This approach can be applied to all levels of Johnson's (1980) habitat hierarchy, but is probably most applicable to his second- and third-order levels of habitat selection. When applied to the second-order level, analyses focus on comparing the proportional use versus availability of different cover types. If a species demonstrates disproportional use of one cover type over others, then selection is inferred for that type. A number of analyses are available for these tests, each with various advantages and disadvantages (cf., Alldredge and Ratti, 1992).

Comparisons of use and availability on Johnson's (1980), third-order level entail contrasts of habitat components in areas where birds are found (i.e., focal-bird plots) with a random sample of habitat components (e.g., Brennan et *al.*, 1987). Univariate or multivariate analyses can be done to show how the species uses various habitat components nonrandomly. Perhaps the primary difference between the two different levels of use-availability analysis is that the second-order level examines use among cover types, whereas the third-order level details within-stand habitat use.

Fagen (1988) suggested that the ratio of habitat use:habitat availability could be viewed as an index of habitat quality under the assumption that animals were free to choose habitats that conferred the greatest fitness.

Hobbs and Hanley (1990) tested this relationship and found that habitat quality could not be measured using this simple ratio because habitat availability changed constantly through time and space. This conclusion essentially agrees with that of Van Horne (1983), who showed that density alone was a misleading index of habitat quality. Consequently, results of use–availability studies should be viewed simply within the context of habitat use and not indicative of habitat suitability or quality.

4.4. Food Resource and Habitat Use

The distribution and abundance of food also influence habitat use. For example, if food is patchily distributed, a species may be restricted to only a portion of its potential habitat. The abundance of food may directly influence abundances (i.e., numerical response) of birds present (Morris et *al.*, 1958; Koplin, 1972). Much of optimal foraging theory attempts to explain how the distribution, abundance, and quality of food influence distributions, habitat use, and movements of birds. Thus, it is well documented that food is one of the primary factors underlying habitat use by birds.

One aspect of contemporary avian habitat analyses that has begun to receive well-deserved attention is examining relationships between food resource abundance and habitat use. The series of papers in the recent symposium proceedings on foraging methodology provides an excellent overview of this topic (Morrison et al., 1990).

Two problems arise with this sampling of food resources, however. First, it is difficult to determine whether or not a certain resource is available to the birds being studied. Sampling insects that dwell in a forest canopy and relating their distribution and abundance to habitat use patterns of birds is a classic example of how observer-defined "availability" of resources can bias a study (Morrison et *al.*, 1990). This is because the observer is sampling resources from a perspective that he assumes is important to the bird. Analyses of frugivory are plagued by similar biases. The second problem is the difficulty in obtaining an unbiased sample of the food resources. Usually several sampling methods are needed to quantify the major arthropod groups fed upon by one or more bird species (Morrison et *al.*, 1989). The logistics of sampling even one major group are formidable; if they are done adequately, an investigator can spend more time in arthropod sampling than in all other tasks combined! Obtaining accurate assessments of relationships between bird habitat use and food abundance is also influenced by the complexity of the vegetation. Clearly, it is much easier to survey potentially available food resources in a grassland system, where the entire habitat is less than 2 m in height, than in a forest where the tree canopy may exceed 40 m.

5. CASE HISTORIES OF HABITAT CONCEPT APPLICATIONS: CONTROVERSIES AND OPPORTUNITIES

Various aspects of the habitat concept have been applied to the study and management of birds. Indeed, much of the foundation of avian ecology is based on eludicating characteristics of the physical environments where birds are found. Further, management of birds and their populations is predicated upon providing suitable conditions for their persistence. This is particularly the case for threatened, endangered, and sensitive species. We provide examples using the Red-cockaded Woodpecker (Picoides borealis) and the Spotted Owl to demonstrate how habitat provides a basis for the management of such species. Habitat concepts also provide bases for explaining the extant status of many species of birds. For example, much of the perceived decline in neotropical migratory birds is thought to be attributable to habitat loss and fragmentation. We describe in Section 5.3 how these factors are related to declines in neotropical migrant bird populations. Finally, we would be remiss by not discussing how habitat has played a central part in gamebird management. Many of the philosophies of present-day wildlife management are rooted in techniques first developed for game management. A fuller understanding of the contemporary perception of avian habitats is indeed enhanced by recognizing some of its roots.

The case histories that we present in the following sections are not intended to be full treatises on how concepts of habitat have been incorporated into avian research and management. Instead, we offer them as examples of how some concepts have been and can be used in ornithology and management. We view these as opportunities influencing future directions in applications of the habitat concept in ornithology.

5.1. Red-cockaded Woodpecker

The Red-cockaded Woodpecker has been the center of a forest management controversy in the southeastern U.S. for the past two decades (Ligon et al., 1985, 1991; National Wildlife Federation, 1990). The controversy started because the specific habitat needs of this bird conflicted with standard southern forest management practices (Ligon et al., 1985, 1991). Red-cockaded Woodpeckers require mature (60+ years) open, parklike pine (*Pinus* spp.) forests that are maintained by recurring fire (Ligoin, 1970; Hooper et al., 1980; Jackson, 1981, 1986). However, modern timber management practices in the southeastern U.S. emphasize production and harvest by clearcutting before stands develop the characteristics needed by this species. The loss of habitat wrought by these forestry practices, along with the widespread exclusion of fire, caused Red-cockaded Woodpecker populations to decline throughout the southeastern U.S. until they were federally listed as endangered. Red-cockaded Woodpecker populations have continued to decline since passage of the Endangered Species Act in 1973 (Ligon et *al.*, 1985,1991). The most likely reason for the continued decline is the continuing loss of habitat over substantial portions of the species' range. This habitat loss has occurred through stochastic events such as hurricanes and continued harvest of suitable habitat on private lands where approximately 75% of remaining suitable habitat occurs (U.S. Fish and Wildlife Service, 1985; Ligon et al., 1985). Today, most efforts to enhance and maintain Red-cockaded Woodpecker habitat are done on public lands, usually National Forests and/or Wildlife Refuges that are regulated by multiple-use management policy (Ligon et *al.*, 1985). These habitat-management efforts for the Red-cockaded Woodpecker on public lands are likely to intensify during the next decade, especially if the Emergency Action Plan (National Wildlife Federation, 1990; Ligon et *al.*, 1991) outlined in the proceedings of the recent Scientific Summit on the Red-cockaded Woodpecker is implemented.

Although a great deal of research effort and attention has been focused on the Red-cockaded Woodpecker since the early 1970s, there are still a myriad of questions about the biological and ecological processes that influence populations of this bird (Ligon et al., 1985; National Wildlife Federation, 1990). Most questions pertain to population dynamics, long-term viability of different-sized colonies, and the best strategies for reestablishment of abandoned colonies. Additionally, no published data are available on the effects of Red-cockaded Woodpecker habitat management on other, nontarget vertebrate populations.

The need for an integrated, ecosystem approach to Red-cockaded Woodpecker research and management is a theme that recurs throughout the Reports of the American Ornithologists' Union Committee for the Conservation of the Red-cockaded Woodpecker (Ligon et al., 1985, 1991) and the Proceedings of the Scientific Summit on the Red-cockaded Woodpecker (National Wildlife Federation, 1990). Managing for the Red-cockaded Woodpecker, as a "keystone species," equates to managing an entire forest ecosystem (National Wildlife Federation, 1990:7). However, we currently have no information about how Red-cockaded Woodpecker habitat management influences the distribution and abundance of forest vertebrates in the southeastern U.S. Other terrestrial vertebrate species that have been experiencing long-term population declines in the southeastern U.S., including Bachman's Sparrow (Aimophila *aestivalis*), Fox Squirrel (Sciurus niger), Gopher Tortoise (Gopherus polyphemus), Indigo Snake (*Drymar*chon coraris couperi), and Northern Bobwhite (Colinus virginianus) (Brennan, 1991a) may benefit from Red-cockaded Woodpecker habitat management because these species apparently have habitat affinities with open, parklike, mature pine forests that are maintained by frequent fires. However, we will have no way of knowing the larger impact of Red-cockaded Woodpecker habitat management on these and other terrestrial vertebrates until research is initiated to evaluate these effects.

Curiously, scant attention has been paid to modeling habitat relationships of terrestrial vertebrates in pine and mixed-pine hardwood forests of the southeastern U.S. Neither the Red-cockaded Woodpecker nor associated models of vertebrate habitat relationships in the forests of the southeastern U.S. are mentioned in the proceedings of the most recent international habitat modeling symposium (Verner et al., 1986). Recent successful development of a cost-effective artificial nest-cavity insert (Allen, 1991; Copeyon et al., 1991) now means that it is possible to manage habitats for the Red-cockaded Woodpecker on a scale previously thought to be impossible. Now that managers know how to manipulate this key habitat component, it may be possible to stabilize or increase Red-cockaded Woodpecker populations. The only remaining obstacle is the need for a wholesale change of attitude toward Red-cockaded Woodpeckers by forest managers in the southeastern U.S. Future research should investigate development of innovative harvest techniques that will enhance conservation of woodpecker populations in managed forests.

5.2. Spotted Owl

The Spotted Owl occurs in forested environments of the western United States. Three subspecies are recognized: the Northern (S. o. caurina), California (S. o. occidentalis), and Mexican (S. o. lucida) spotted owls. Currently, the Northern Spotted Owl is regarded as a federally threatened subspecies and the Mexican subspecies has been proposed by the U.S. Fish and Wildlife for listing as a threatened species. Although no formal listing procedures currently exist for the California Spotted Owl, such actions will likely occur in the near future.

Most data on the habitat ecology of the Spotted Owl suggest that it requires mature forest conditions to meet its life-history requirements (Forsman et al., 1984; Ganey and Balda, 1989; Solis and Gutierrez, 1990). Mature forests provide suitable nest structures (LaHaye, 1988; Buchanan, 1991), roost sites (Solis and Gutierrez, 1990), prey abundances (Carey et al., 1990; Ward, 1990), and microclimatic conditions (Barrows, 1981). Typically these birds require expansive home ranges, ranging from 500 to 2500 ha.

Conflicts arise because the Spotted Owls use the same forests that contain commercially valuable timber. In contrast to the Red-cockaded Woodpecker, most Spotted Owl habitat occurs on public lands. Logging practices on these lands have tended to fragment owl habitat by reducing the absolute quantity of Spotted Owl habitat while reducing stand sizes, altering stand shape, and increasing distances between suitable habitat. Most data suggest that forestry practices are not compatible with the population viability of Spotted Owls. Much of the economy of the Pacific Northwest is based on the timber industry. Thus, the forests contain both ecological and economic values that are often incompatible under present-day management strategies.

An interagency panel of scientists was assembled and given the charge of developing a conservation strategy for the Northern Spotted Owl. This panel, chaired by Jack Ward Thomas of the U.S. Forest Service, included representatives of the U.S. Fish and Wildlife Service, Bureau of Land Management, state wildlife agencies of Oregon and Washington, the U.S. Forest Service, and various conservation groups. This panel assembled all known information on the ecology of the Spotted Owl. Where key information was lacking, the team developed sophisticated models to predict those relationships. The panel considered all information and developed a plan for the conservation of the owl. This plan is undoubtedly the most comprehensive, state-of-the-art plan developed for any vertebrate species. It incorporated principles of habitat and population ecology and applied them across the landscape. The underlying objective of the plan was to provide for long-term population viability of the owl (Murphy and Noon, 1991). Thus, the foundation of the plan included mechanisms to provide gene flow and the maintenance of genetic variation. The basic premise of the plan was to manage for owl habitat and to provide a framework to ensure the existence of owl habitat in the future. This plan undoubtedly will provide a template from which future conservation plans will follow.

The plan calls for the establishment of "Habitat Conservation Areas" (HCAs), large enough to support 20 pairs of owls. The 20-pair criterion was based on models of population ecology that specified that this number of pairs was the minimum number for a population to persist. HCAs were clumped to permit dispersal across relatively short distances (up to 20 km), and thus provide mechanisms for adequate gene flow. Guidelines were proposed for the management of lands intervening among HCAs to ensure appropriate conditions for dispersing birds. The geographic extent of this conservation plan included all known and potential owl habitat found on public lands in northwestern California, Oregon, and Washington. Undoubtedly, the plan is the most comprehensive one developed to date. Whether or not the plan will be effective in conserving the Spotted Owl is unknown. At this point, the conservation plan is conceptual. The plan is based on a set of assumptions, the validity of which is unknown. As with any model, it must endure an interactive process of testing, refining, and testing again. As the model is implemented and refined, the ultimate test will be if populations of Northern Spotted Owls persist through time.

An alternative Spotted Owl Management Plan, developed by the National Forest Products Association and American Forest Council (Anderson et *al.*, 1992) plans to reduce the current number of extant owl pairs by over 60%. This plan fails to consider vast areas of occupied and potential owl habitat in the Coast Ranges of California, Oregon, and Washington, and furthermore relies on National Parks and Wilderness Areas for maintaining the majority of future owl habitat. Curiously, this plan ignores all of the best available demographic information on this bird. If implemented, this plan may spell disaster for the owl. If nothing else, such a document illustrates the dangers of how a conflict of interest can compromise what should be an objective application of the habitat concept.

5.3. Neotropical Migrant Birds

In the western hemisphere, neotropical migrant birds are typically those that breed in temperate environments of North America and winter in tropical environments of Mexico and Central and South America. En route to and from the breeding grounds, these birds use a variety of habitats during migration. Recent analyses of U.S. Fish and Wildlife's Breeding Bird Survey data indicate that populations of many species are exhibiting declines (Sauer and Droege, 1990; Finch, 1991). Reasons for these declines are not entirely clear, although habitat loss and fragmentation both on temperate breeding and tropical wintering grounds appear to be the primary underlying factors. Quite likely the cumulative effects of all factors are just beginning to become apparent. The population declines of these species are particularly alarming because of their extensive nature, occurring across the continent. Below, we discuss some of the empirical data and suggested hypotheses concerning these declines.

Widespread and local human activities have altered the natural landscape at rates that far exceed the ability of many species to adapt or even adjust to the changes. A major concern today is the effect of forest fragmentation on the population and distribution of birds. Forest fragmentation commonly results from forestry practices that modify stand structure and landscape patterns by altering stand size and shape, and the distance between stands. If we confine our discussion to forests undisturbed by modern forestry practices, then the effect of fragmentation is more directional in that it decreases the size of stands of such forest while increasing the distance between stands. Concomitantly, the amount of disturbed forest increases and the distance between them decreases. Thus, species that find suitable habitat primarily in undisturbed forests will experience a decline in the total amount of potential habitat and species that require large blocks of habitat will find fewer of those blocks available (Robbins et *al.*, 1989). The area between these undisturbed stands will increase, thus creating barriers to movements of individuals from one patch to another.

The exact effects of habitat fragmentation and patchiness on the distribution of birds are not completely resolved. Loss of total habitat area and fragmentation are clearly related, but each might affect bird populations in different ways (Lovejoy et al., 1986; Haila and Hanski, 1984). Most information is from eastern deciduous forests that have undergone human-induced impacts for far longer than western forests. Harris (1984) and Rosenberg and Raphael (1986), however, have examined the effects of forest fragmentation on vertebrates in western coniferous forests. Fragmentation often results in increased species richness largely because of greater numbers of edge species (Whitcomb et al., 1981; Blake and Karr, 1984). These species increase because fragmentation effectively creates edge habitats, providing these species with more habitat than present prior to fragmentation. Conversely, fragmentation decreases the size of contiguous forest stands. Some species of birds require large tracts of forest and are generally termed "forest-interior-dwelling" species (Temple, 1986). Populations of many of these species may be declining as a result of less habitat available for occupancy and increased vulnerability to nest predation and brood parasitism (Robbins et al., 1989). Further, fragmentation also increases the distance between stands. Whitcomb et *al.* (1981), Lynch and Whigham (1984), and Askins et *al.* (1987) noted an inverse relationship between the number of forest-interior species and distance between stands. This relationship may be a result of extensive barriers to dispersal.

Unfortunately, far too little is known about the habitat requirements of most neotropical migrant bird species. Without these data, managers are unable to effectively manage their lands for these birds. An agenda must begin now to address this problem and provide solutions before many of the species become locally extirpated or even extinct.

In this regard, the Neotropical Migratory Bird Conservation Program was developed (Finch, 1991). This program includes cooperators from most federal and state resource agencies and many nongovernmental organizations. Among the objectives of the program are to determine trends in bird populations and habitats, identify factors underlying population declines, and develop plans for the conservation of neotropical migrants.

5.4. Game Birds

Because of their value as a consumptive resource, a great deal of ornithological research has been conducted on relationships between game birds and their habitats. Here, we will illustrate how some classic studies of galliforms and anseriforms have contributed to the development of the habitat concept.

Prior to the development of wildlife management as an academic discipline during the early 1930s (Leopold, 1933), virtually all of the original research on game birds was published in the ornithological journals or as monographs (e.g., Grinnell et al., 1918). However, the initiation of specialized outlets for applied wildlife management research, such as Journal of Wildlife Management, and the Transactions of the North American Wildlife and Natural Resources Conference, provided opportunities for game bird biologists to publish results of their studies in outlets other than the traditional ornithological journals. During the past several decades, a rift seems to have developed between game bird biologists and "traditional" ornithologists. These two groups seem to have diverged to the point where there is minimal interaction among scientists from both camps. For example, recent programs at annual American Ornithologists' Union meetings have scheduled waterfowl papers into separate sessions, rather than spread them out through the entire program. The result of this is that waterfowl biologists end up talking to an audience of waterfowl biologists and there is minimal opportunity for cross-discipline transfer of ideas among ornithologists. Therefore, our goal in this section is to give the reader an appreciation of how game bird studies have contributed to the development of the habitat concept in ornithology.

5.4.1. Galliformes

Stoddard (1931) was probably the first modern ornithologist to establish that habitat components could be manipulated to increase population abundances of birds. Although heretical at the time (Stoddard, 1936), the use of prescribed fire as a key component of Northern Bobwhite management has become a commonly accepted practice for sustaining habitats of other birds such as Kirtland's Warbler (Dendroica *kirtlandii*), Red-cockaded Woodpecker, and Bachman's Sparrow.

Leopold (1944) established a physiological basis for survival of birds that had been translocated into new and/or vacant habitats. Biologists were perplexed at the failure of Wild Turkey (Meleagris gallopavo) introductions when domesticated or domestic x wild hybrids were used. Leopold established that native Wild Turkeys had larger brains, adrenal glands, and pituitary glands than either domestic or hybrid turkeys. He linked these physiological differences to behaviors such as wariness, and quickness of predator evasion, that apparently help birds survive in the wild. Thus, Leopold (1944) used the Wild Turkey as an example of how physiological parameters can influence the survival of an organism when it is translocated into new or different habitats. This study has profound implications for any program where the goal is to reestablish populations of wild birds in appropriate habitats.

Biologists working with Wild Turkeys were among the first ornithologists to recognize problems of scale. For example, Mosby and Handley (1943), Kozicky and Metz (1948), and Stoddard (1963) recommended that large (5,000–25,000 ha) blocks of habitat were essential for successful translocation of Wild Turkeys into unoccupied habitat. Additionally, Mosby (1949) was among the first biologists to recognize that control of harvest (both legal and illegal) was essential if populations were to have a chance to respond to habitat management and manipulation.

Research on Ruffed Grouse (Bonasa umbellus) by Gullion and Marshall (1968) provided one of the first examples that documented differential survivorship of a species of bird in different habitats. They found that grouse survived longer, and were more abundant in stands dominated by quaking aspen (Populus tremuloides). Managing small blocks of aspen in different age classes provides optimum habitat components required to meet the annual cycle needs of the Ruffed Grouse (Gullion, 1972). Additionally, further study of the relationships between Ruffed Grouse and quaking aspen has indicated that chemical composition (levels of coniferyl benzoate and protein) of aspen buds used for food by grouse changes among years and may influence Ruffed Grouse population abundance (Jakubas and Gullion, 1991), thus providing an example of how chemical composition of foods in a habitat may influence survival.

Goldstein (1984) observed that during summer, Gambel's Quail (*Callipepla* gambelii) foraging ecology and habitat use were directly influenced by the daily environmental temperature profile. On excessively hot days during summer, this quail exists in an environment that is near the upper limit of its thermal tolerance. Refugia in vegetation that provides shade during midday heat is apparently the essential habitat component that allows this bird to survive in this environment. Goldstein (1984:549) calculated that Gambel's Quail would reach fatal hyperthermia in just over 1 minute of foraging in ambient temperatures above 45°C, which commonly exist in desert environments during summer. Thus, this quail is able to exist in an extreme environment where potentially lethal factors are buffered by habitat components.

Game bird biologists were among the first ornithologists to use multivariate statistics for studies of habitat relationships and ,development of habitat-suitability index models. For example, Martinka (1972) used discriminant function analysis to describe and synthesize aspects of Blue Grouse habitat. Brennan et *al.* (1986) used data from the study of Mountain Quail habitat relationships to develop the first data-based approach to developing habitat-suitability-index models using logistic regression. One of the few attempts at testing such models has also been conducted using game bird habitat data (Brennan, 1991b).

5.4.2. Anseriformes

Ornithologists who work on waterfowl have been among the leaders in experimental tests of hypotheses related to the habitat concept in ornithology. Although many species of waterfowl migrate over broad distances between breeding and wintering habitat, many species of waterfowl are excellent subjects for manipulative experiments because water levels, vegetative composition, and predators can be manipulated in an experimental context. Beginning with experiments conducted on the cavity-nesting Wood Duck (Aix sponsa) and continuing to present contemporary experimental studies where arrays of environmental components are manipulated (Bailey, 1981; Kaminski and Prince, 1981; and Murkin et *al.*, 1982), waterfowl biologists have clearly set a high scientific standard of experimental examples. Waterfowl biologists continue to cite a need for expanded use of experimentation to test habitat-related hypotheses in ornithology (Clark and Nudds, 1991).

Early work on the Wood Duck indicated that it would be feasible to provide artificial cavities (nest boxes) to increase population abundance and productivity (Bellrose, 1990). The relationship with the habitat concept here is that the lack of a key habitat component was identified and then manipulated for the benefit of the species. Experimental manipulation of the entrance dimensions and configuration resulted in an entrance hole that would permit the ducks to enter, but not raccoons (Procyon *lotor*) (Bellrose, 1955). Additional modifications, such as placement of the boxes on poles in water also helped increase productivity (Johnson, 1947). The success of Wood Ducks with artificial nest cavities has formed a basis for applying this concept to other species such as bluebirds (Sialia spp.).

Kaminski and Prince (1981) manipulated basin surface and cover:water ratios within an impounded meadow in south-central Manitoba. They found that the greatest density and diversity of breeding duck pairs were greatest on experimental plots with a 50:50 cover:water ratio, as opposed to 30:70, or 70:30. In a companion study, Murkin et al. (1982) observed that cover:water ratios also influenced duck and invertebrate abundance on a within-season temporal scale. Ball and Nudds (1989) continued on this experimental track and found that, for Mallards (*Anas* platyrhynchos) the optimum size of openings in a 1:1 ratio of cover:water was approximately 0.15 ha. Such experimental studies provide an example of the inferential power, and progression of knowledge that can be gained by applying experimental methods to the study of avian habitat relationships. They also demonstrate that waterfowl biologists have been among the leaders in developing new knowledge about the habitat concept in ornithology.

This section is by no means a complete or exhaustive survey of game bird studies that have contributed to our understanding of the habitat concept. Rather, it is an attempt to point out some examples from the literature to support our contention that examples from the game bird literature are often overlooked when it comes to citing examples that contribute to our search for generalizations in ornithology.

6. SYNTHESIS

6.1. What Do We Really Know about Birds and Their Habitats?

In most cases, we probably know less than we think we do about birds and their habitats. Any study of avian habitat relationships must pass through a series of multiple, anthropocentric filters that will ultimately bias the results to an unknown degree. Nevertheless, this is not a legitimate reason to abandon avian habitat ecology and take up less meaningful pursuits. Given the pace of increasing urban development, and deteriorating environmental quality, we are facing a critical need for reliable information on birds and their habitats on virtually all levels.

On the most basic level, we know that virtually every species is most likely unique in how it responds to components of its environment. Additionally, we know that it might be possible to integrate, through adaptive, ecosystem-scale management the needs of multiple species. Beyond these two basic notions, it seems that we really don't know much at all about birds and their habitats. Decades of sophisticated, quantitative analyses have done little to improve on the qualitative observations of the pioneering, New World naturalists.

Ornithologists continue to add to a vast storehouse of information on birds and their habitats. Some of this information can be interpreted in light of evolutionary theory, and some may be useful for making predictions and developing strategies to conserve declining populations. Most of this information, however, is extremely fragmented, superficial, and in many cases suffers from bias and imprecision. MacFayden (1975) used the metaphor of "being washed out to sea on an immense tide of unrelated information" to describe problems facing contemporary habitat ecologists. Southwood's (1977) claim that our lot is comparable to that of the inorganic chemist before the periodic table remains true even today.

6.2. How Can We Improve Future Avian Habitat Studies?

So what can we do? First, we need to accept the stochasticity and variation that is part and parcel to most relationships between birds and their habitats. Ecological data on avian habitat relationships are often highly skewed and bimodal, and rarely, if ever, meet parametric statistical assumptions. Think of this as an opportunity rather than a liability. Ornithologists will probably never be able to make predictions that are comparable to landing a piece of machinery on the square kilometer parcel of the moon.

We need to train focused, critical eyes, and skeptical minds on the problem at hand when we design avian habitat studies and interpret the resulting data. We need to avoid any pretense that a complex mathematical analysis will somehow substitute for a poor or nonexisting design or a vague hypothesis. We need to pose the right questions. We need to conduct experiments whenever possible with adequate replication to ensure reliable results. We need to use sampling techniques that are quantifiable, reliable, and repeatable. We need to determine how many samples are required for a required level of precision so that precious research dollars are not wasted by collecting two few or too many samples. Most importantly, we need to realize that the habitat concept is one of the few unifying notions available to ornithologists.

ACKNOWLEDGMENTS. We thank J. B. Buchanan, R. J. Cooper, R. M. Kaminski, R. W. Mannan, M. L. Morrison, K. L. Purcell, J. P. Ward, and students of the Wildlife Biology group at Mississippi State University, for reviewing earlier drafts of the manuscript. We also thank J. Gomez and T. Pruden for providing editorial assistance, and J. Heard of the Information Services Department at Mississippi State University for drafting figures.

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