

Habitat Ecology

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THE NORTHERN SPOTTED OWL: A PREVIEW OF LESSONS IN AVIAN HABITAT ECOLOGY

The Northern Spotted Owl (*Strix occidentalis caurina*) is one of the most well-studied bird species in the world (Gutiérrez et al. 1995, USFWS 2011), and also one of the most controversial. Conflict between conservationists and the timber industry erupted in the 1980s over the spotted owl's association with economically valuable old-growth forests of the Pacific Northwest in North America (Yaffee 1994), leading to debates, lawsuits, death threats, and eventually the large-scale ecosystem management plan called the Northwest Forest Plan (Davis et al. 2011). This owl has become a poster child for the tension between traditional environmentalism and economic development (Gup 1990). Habitat ecology is the centerpiece to bird conservation and is at the heart of the spotted owl saga; the owl's story provides a preview of seven major lessons of this chapter (fig. 18.1).

The Northern Spotted Owl is a denizen of old forests of the Pacific Northwest—places dominated by large coniferous trees, such as Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), and complex forest canopies with dead or damaged trees and downed logs (e.g., Forsman et al. 1984). But knowledge of simple habitat associations is insufficient. Spotted owls use forests with large (usually old) trees at several spatial scales (from nest trees to landscapes; Blakesley et al. 2005), but the availability of safe nesting sites and rodent prey underlie the selection of forest attributes (Sakai and Noon 1993, Zabel et al. 1995). These studies of spotted owl habitat associations highlight the first two lessons of this chapter: (1) We must be mindful that habitat is more than the vegetation around a bird; it is rooted in the resources and ecological conditions a bird needs for survival and reproduction. And (2), to balance species conserva-

tion and human needs, we must understand the nuances of “habitat selection”—the study of where birds live and why. Indeed, Franklin et al. (2000) found that in Northern California, where spotted owls eat woodrats (*Neotoma* spp.) associated with young forests and forest edges, owl reproduction and survival was highest where owl territories were composed of a mosaic of old and young forests that provide large trees for nesting and young patches with abundant prey. Such findings illustrate another lesson: (3) Estimating the capacity for a habitat to support survival and reproduction is arguably the best way to measure habitat quality (Johnson 2007). This work proved central to understanding spotted owl demography (USFWS 2011) and underscored a fourth major lesson: (4) The quality, quantity, and spatial distribution of habitats strongly influence population dynamics for



Figure 18.1. Northern Spotted Owls (*Strix occidentalis caurina*). In this photo, you can see colored leg bands used to mark these birds for studies of their habitat and population dynamics, in this case on the Hoopa Valley Indian Reservation in Northern California. Photo by J. Mark Higley, Hoopa Tribal Forestry.

many bird species in the world (Newton 1998). The profound role of habitat in spotted owl conservation has prompted extensive research to map the distribution of the owls and their habitats. These maps began as simple hand-drawn range limits based on aerial imagery, but with the rapid improvement of statistical and spatial models (Elith et al. 2006, Phillips et al. 2006) and advances in remotely sensed data (e.g., high resolution satellite imagery; Ackers et al. 2015), avian ecologists are now producing high-resolution maps of bird distributions over broad spatial and temporal extents (e.g., Schumaker et al. 2014) including for the Northern Spotted Owl (Stralberg et al. 2009b). This provides another lesson for contemporary ornithologists: (5) New technologies can be harnessed to help measure habitat selection and habitat quality, and to map habitats in novel ways. However, with new technologies come discrepancies in their application, and controversy among owl researchers continues today over how to best link habitat selection, maps, and demography in order to further conservation goals (Loehle et al. 2015, Dunk et al. 2015, Bell et al. 2015). These are not just academic arguments, because conservation and land-use rules rely on accurate and meaningful maps of spotted owl habitat. This reliance exemplifies another lesson: (6) Habitat ecology strongly affects environmental policies, which carry enormous social and economic consequences. In fact, the term “critical habitat” is a keystone to the US Endangered Species Act (Camaclang et al. 2015), arguably the most powerful piece of wildlife conservation legislation in the world. In a landmark decision involving both Northern Spotted Owls and Red-cockaded Woodpeckers (*Leuconotopicus borealis*), the US Supreme Court confirmed that destroying critical habitat is just as serious as killing birds directly (*Babbitt v. Sweet Home* 1995). This decision not only represented a huge shift in environmental law and prompted modern wildlife conservation (Kareiva and Marvier 2015), it also exemplifies the relationship between science and law (Alagona 2013) evident in recent summaries of spotted owl conservation plans by the US Fish and Wildlife Service (USFWS 2011, 2012).

So where does this story end? There is both reason for concern and cause for celebration regarding the Northern Spotted Owl. Thankfully, a better understanding of habitat ecology has enabled modern forestry to, in some places, integrate timber extraction and owl habitat conservation (e.g., Forsman et al. 2011). However, the spotted owl needs more than just sufficient high-quality habitat. Demographic modeling has revealed the importance of local weather and climate, with cold wet winters diminishing owl reproduction (Franklin et al. 2000, Dugger et al. 2005, Glenn et al. 2011). Old forests may provide some protection from inclement weather, but these findings

raise the specter of how this species may fare under ongoing climate change (Carroll 2010). Added to the list of challenges facing this bird is the looming advance of a closely related species, the Barred Owl (*Strix varia*), into the spotted owl’s range. Barred Owls appear to outcompete and depredate spotted owls in most, if not all, habitats (Wiens et al. 2014), and the Northern Spotted Owl continues to decline in most of its range (Forsman et al. 2011). Thus, despite the enormity of research on spotted owl habitat ecology, the latest findings reveal a final important lesson: (7) Other factors can interact with or in some cases overwhelm habitat in driving bird populations, and ornithologists must be aware of the range of processes affecting birds.

In this chapter, you will come to recognize the theory underlying these seven lessons illustrated by the story of the Northern Spotted Owl. First, we examine core definitions of habitat ecology and learn about the history of the discipline. Next, we introduce theories of habitat quality and selection before considering the consequences of habitat to bird populations. Then we explore some common methods for studying bird habitat, both in the field and with remote measurements. The chapter concludes with the implications of habitat ecology for modern avian conservation. Throughout, you will gain an introduction to the field of avian habitat ecology, becoming familiar with its development, importance, and opportunity, and its limitations.

HABITAT: ITS CORE DEFINITION AND RELEVANCE

As the story of the spotted owl illustrates, habitat is central to bird conservation because the resources and environmental conditions in a habitat affect birds’ survival and reproduction (Bernstein et al. 1991, Pulliam 2000). It is no surprise, then, that ornithologists have long recognized the need to understand variation in habitat for birds (Block and Brennan 1993). Indeed, there is overwhelming evidence that the loss and degradation of habitat poses the greatest threat to bird species (fig. 18.2).

Despite the centrality of habitat to the discipline of avian ecology, confusion remains over how to best measure variation in habitats over space and time. Hall and her colleagues (Hall et al. 1997, Morrison et al. 2002) argued that some of this confusion stems from inconsistent and imprecise use of terms, which is unsurprising, given habitat’s long history in ecology (Grinnell 1917, MacArthur et al. 1962, Whittaker et al. 1973, Johnson 2007). Hall et al. (1997) sought to provide standards, emphasized that habitat is species-specific, and established a **definition of habitat** as “the resources and conditions present in an area that produce occupancy—including

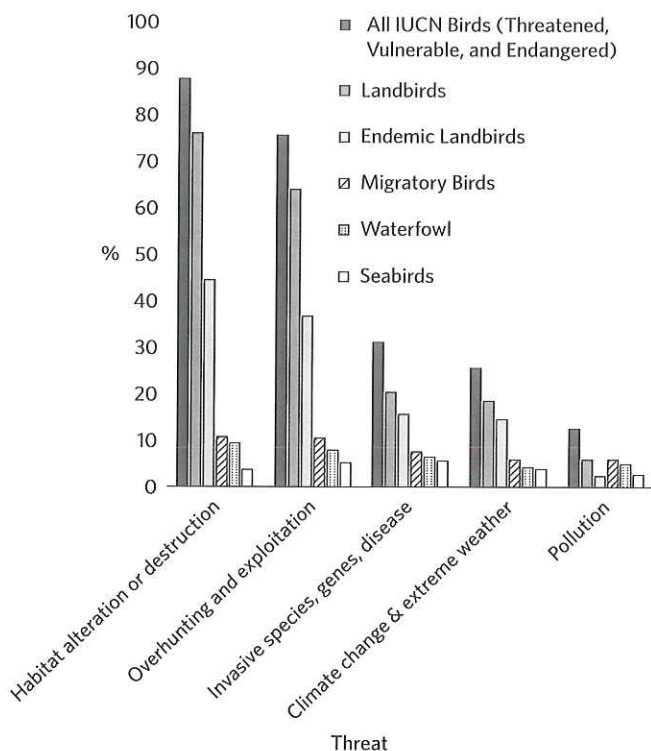


Figure 18.2. The top five threats facing birds species in the world, according to the International Union for the Conservation of Nature (IUCN) Red List of bird species (near threatened, vulnerable, and endangered, $n = 2,364$). Numbers sum to more than 100 percent because a species can be affected by more than one threat. Habitat alteration or destruction is the overwhelmingly most common threat faced and includes the following categories of human activity: agriculture and aquaculture, energy production and mining, human intrusions and disturbance, residential and commercial development, and transportation and service corridors.

survival and reproduction—by a given organism.” This is the definition of habitat used in this chapter. Sometimes, habitat is crudely described as the vegetation where a bird species is typically found—e.g., bottomland hardwood habitat, tall grass prairie habitat, estuary habitat (Hutto 1985). This definition is of limited value because it depends on classification of often continuous resources or conditions into discrete categories, and it does not address the issue of habitat quality (Gaillard et al. 2010). Further, that definition does not recognize that habitat is species-specific, and it is insensitive to spatial and temporal scales. As the lesson of the spotted owl showed, we must be mindful that habitat is more than the vegetation around a bird; it is rooted in the **resources** and **ecological conditions** a bird needs for survival and reproduction. By studying the resources (e.g., food, cover, and nesting sites) and ecological conditions (e.g., climate, predation risk, and competition), we can better understand what

birds need. Critics of habitat ecology rightly emphasize that ornithologists too often rely on simple vegetation classifications, and that research should instead strive to focus on resources and constraints affecting bird fitness (Romesburg 1981, Morrison 2001).

Historical Perspective

Ornithologists have contributed substantively to the development of the habitat concept, perhaps in part because birds are generally conspicuous and easy to observe in their habitats, and they lay eggs in discrete nests that enable quantification of reproductive rates (Rotenberry 1981, Block and Brennan 1993). The primacy of habitat in ornithology has resulted in several eras of avian habitat ecology: cataloging habitats and natural history (box on page 581), quantitative ecology, wildlife–habitat relationships, and, most recently, spatial habitat modeling. We briefly summarize these eras here. For more comprehensive reviews of this history, see Karr (1980), Block and Brennan (1993) and Stauffer (2002).

The cataloging and natural history eras of habitat ecology began with Aristotle, with basic descriptions of the vegetation commonly associated with animals (Mayr 1982). It peaked with the insight and synthesis offered by Joseph Grinnell and his colleagues and students (Morrison et al. 2012). During this broad span of time, ornithologists made increasingly sophisticated qualitative descriptions of animals’ habitats, with later work offering the lasting contribution of posing testable hypotheses about ecological factors that may, over evolutionary time, influence the distribution and adaptations in birds (Block and Brennan 1993).

The era of quantitative habitat ecology was prompted by the seminal work of Hutchinson and his student MacArthur. Hutchinson (1957) introduced the modern concept of a multidimensional ecological niche, meaning that several resources axes (such as gradients in forest canopy cover, elevation, and insect abundance) could describe a theoretical space within which a bird species can persist. MacArthur (1958) advanced these ideas with his classic study of eastern wood warblers (*Parulidae* spp.), showing that species use different habitats within the trees of eastern forests and bolstering the notion that species distributions are governed by the combined effects of biotic and abiotic factors.

The advent of more powerful computers propelled quantitative habitat ecology further, enabling sophisticated analyses of birds and their habitats. The work of James and her colleagues (e.g., James and Shugart 1970, James 1971, James and McCulloch 1990) is exemplary in that she used multivariate statistics to operationalize Hutchinson’s niche ideas (Stauffer 2002). These advances triggered an era of wildlife habitat relationship studies that continued and evolved through the

MARGARET MORSE NICE

By Dr. Chris Tonra, The Ohio State University

Ornithologists and bird enthusiasts often are captivated by the exotic and rare, but it is more often in the common and ubiquitous that the complexity of nature is best examined. While in the early twentieth century ornithology was a field focused on lengthening the species list from far-flung locales, one woman saw the incredible discoveries that could be made in one's own garden. Margaret Morse Nice produced a sea change in ornithology by peering into the (not so) mundane daily lives of the birds we see every day.

In 1927, already an accomplished ornithologist and naturalist, Nice moved to Columbus, Ohio, after her husband took a faculty job at Ohio State University. Her family settled near the banks of the Olentangy River. They chose a home not for good construction, or immaculate grounds, but for the "great weed tangle that stretched between the yard and the river" that she called Interpont. The following spring, when she began banding her yard birds, she captured two birds that would change her life, and an entire scientific field: the male Song Sparrows (*Melospiza melodia*) she named Uno and 4M. Over the next nine years Nice spent countless hours watching these birds and their mates, neighbors, and decedents. She pulled back the curtain on a bird species in ways that had never been done before. As she put it: "Incredible as it may seem, almost complete ignorance reigned as to the life history of this abundant, friendly, and well-nigh universally distributed bird. I went to the books and read that this species has two notes beside the song, and that incubation lasted ten to fourteen days and was performed by both sexes—meager enough information and all of it wrong."

In her time watching and recording her observations of the Olentangy Song Sparrows she introduced ornithology to the complexity of avian territorial interactions and how despotic behaviors (often displayed by the "truculent and meddlesome" 4M) play a role in spatial arrangements. In the field of behavior she described individual variation in song repertoires, the fluidity of pair bonds, antipredator/parasite behavior, brood parasite behavior, and post-fledging care. She described studying the nest behavior and delineation of territories of songbirds, foreshadowing modern methods of monitoring breeding success and density (see example of one of her territory maps, right). In the words of the eminent German ornithologist Ernst Mayr, she "almost single-handedly initiated a new era in American ornithology and the only effective counter movement against the list-chasing movement."

Nice's gift of her words in communicating the wonder of these everyday birds to the rest of the world was in many ways as great as her contributions to science. She published hundreds of writings, many of them for public consumption, which engaged people in the appreciation of birds and bird-

watching. It was her personal connection to the individual birds she followed that informed this passion. After the death of 4M she wrote: "For seven years I devoted myself to the study of the Song Sparrow. During the seasons of alternating hope and discouragement, fulfillment and bitter disappointment, there had been one great blessing—the dauntless cheer of this precious bird and the miracle of his long life." Translating these experiences into her writings, scientific and otherwise, made this 15-gram, drab little sparrow world famous. Nice often bucked convention with her writings, as she preferred the liberal use of language to paint a picture for the reader. She loathed the loss of colorful language in science, at one time noting, "Unfortunately, especially in the United States, it has become the fashion to write up researches so stiffly, matter-of-factly, and technically that all feeling and atmosphere have been banished from too many of them."

Perhaps most importantly, Nice became a high-profile influential woman in the male-dominated world of science in the first half of the twentieth century, in the process becoming an inspiration to young female science enthusiasts everywhere. Today the American Ornithologists Union annually gives the Margaret Morse Nice Award for research by female graduate students, and the Wilson Ornithological Society named its highest honor, for career achievements in ornithology, the Margaret Morse Nice Medal. Nice left an amazing and inspiring legacy when she left the world in 1974 to join 4M, Uno, and the many other birds whose lives she shared with the world. Not bad for spending time sitting on a camp stool under a maple tree with a notebook and "bird glasses," watching the sparrows in the garden.

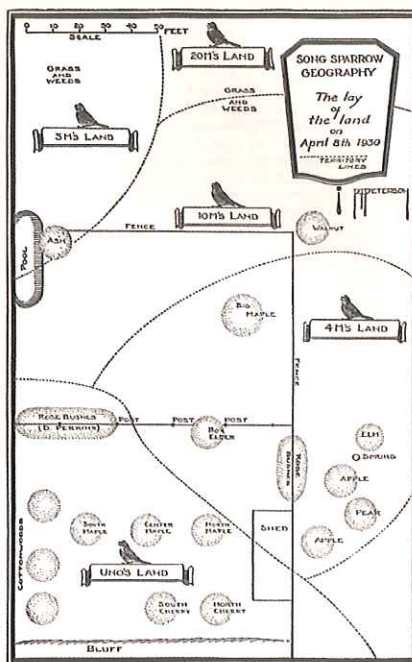


Figure from Nice 1967. Illustration by Roger Tory Peterson. Used by permission of the publisher.

1980s and 1990s (Verner et al. 1986, Scott et al. 2002) and paved the way for the emerging discipline of landscape ecology (Forman and Godron 1986) which enabled researchers to examine multiple scales of habitat associations—from the nest site to the entire range.

The current era of spatial habitat modeling combines concepts from the previous eras with large scale information from remotely sensed habitat data (e.g., from satellite or aerial imagery) and geographic information system (GIS) analyses. In some cases, ornithologists use habitat modeling to test hypotheses about how habitat attributes affect the selection of habitat by birds (e.g., Manly et al. 2002). In other cases, ornithologists conduct analyses to produce maps to predict how birds may respond to future land use changes or anticipated climate change (e.g., Benning et al. 2002, Warren and Seifert 2011). This remains an active field of research and conservation application for ornithologists, and we return to describe current methods later in this chapter.

Documenting where birds are and why they occupy those places is critical for understanding their biology, but ultimately we must link habitat distributions to bird populations to enable effective conservation (Boyce and McDonald 1999, Stauffer 2002). Therefore, alongside the rapid progress in the study of bird distribution, ornithologists have also advanced the study of habitat-specific demography (e.g., Holmes et al. 1996, Rodenhouse et al. 1997, Gaillard et al. 2010), and helped reveal the role of social cues and density-dependence in animals' selection of habitats (e.g., Stamps and Krishnan 2005, Seppänen et al. 2007, Schmidt et al. 2010), concepts we further develop in the following sections.

THEORY FOR HABITAT QUALITY AND SELECTION

Variation in habitat conditions over space and time affect reproduction and survival of individual birds (Brown 1969, Fretwell and Lucas 1970, Sutherland and Parker 1985), and this generates strong selective pressure for birds to select habitat accordingly (Cody 1985). For example, following an abrupt natural decline in the population of European Shags (a cormorant, *Phalacrocorax aristotelis*) on the Farne Islands northeast of England, remaining birds selected among the best available nesting sites, and high rates of reproduction enabled the population to grow until competition forced a greater percentage of birds to occupy poorer sites, pulling down average reproduction (Potts et al. 1980). Thus, the supply of habitat can regulate a bird's population (Newton 1998). It is no surprise, then, that ornithologists work to understand variation in **habitat quality** and **habitat selection** (Block and Brennan 1993, Johnson 2007).

Habitat Quality Theory

Generally, habitat quality is the capacity of the environment to provide conditions appropriate for individual and population persistence (for a more thorough review of habitat quality for birds, see Johnson 2007). While this simple description is intuitive, much is masked by considering habitat quality to relate to both individual- and population-level perspectives (Hobbs and Hanley 1990). For example, in forests of Tennessee that are managed in part for wood production, Boves et al. (2015) found that indicators of habitat quality for Cerulean Warblers (*Setophaga cerulea*) depended on whether they were calculated at the individual level (per capita) or population level (per unit area). In this system, forests that were moderately or heavily harvested were markedly lower in quality than unharvested forest from the perspective of individual birds (per capita rate of reproduction). This result might suggest that unharvested forests should be prioritized in areas targeted for Cerulean Warbler conservation. However, a high density of Cerulean Warblers in some of those same harvested plots more than compensated for the reduced per capita fecundity, so from a land manager's perspective, population-level density and reproductive rates (per unit area) could be maximized in harvested forest. This trade-off in quality and quantity of resources underscores the necessity to distinguish between habitat quality from the perspective of individual animals, which seek to maximize their own fitness, and habitat quality from the perspective of conservationists concerned with populations.

Birds occupying habitats that maximize their lifetime reproductive success will contribute the most to future generations; that is, habitat is a key contributor to an individual's fitness (Block and Brennan 1993, Franklin et al. 2000). Natural selection therefore favors individuals that are capable of distinguishing high- and low-quality habitats (see Habitat Selection Theory, below). Though fitness is an individual measure, Fretwell and Lucas (1970) combined the concepts of habitat and fitness into the notion that a habitat confers fitness on its occupants. Wiens (1992) considered this contribution to an organism's fitness the **habitat fitness potential**, which provides the theoretical basis for an individual-based definition of habitat quality. For example, Franklin et al. (2000) quantified habitat fitness potential for Northern Spotted Owls as the relative contribution to the overall population of individuals occupying a given habitat (fig. 18.3). Thus, habitat quality at the level of an individual bird is defined as the per capita contribution to population growth expected from a given habitat. This conceptualization of habitat quality places evolutionary fitness in a measurable, ecological context with variation that can be quantified over space and

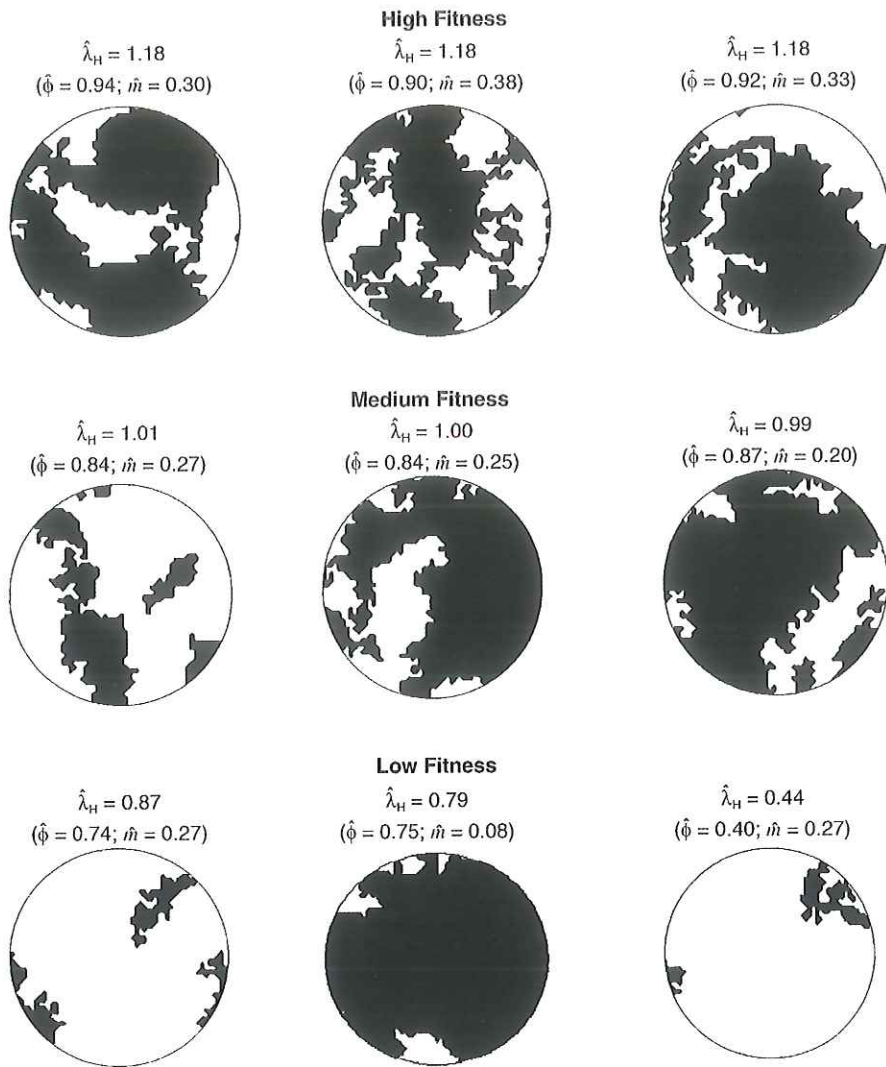


Figure 18.3. Habitat quality for Northern Spotted Owls (*Strix occidentalis caurina*) is highest in territories that are a mixture of old forests for nesting sites and other forests that harbor abundant rodent prey. Circles depict habitat characteristics (within 0.71 km radius circles used to define Northern Spotted Owl territories) at three levels of habitat fitness potential in northwestern California. Dark areas are Northern Spotted Owl habitat; white areas are other vegetation types. Estimates of $\hat{\phi}$ (apparent survival) and \hat{m} (fecundity) are for owls ≥ 3 years old. From Franklin et al. 2000.

time (Coulson et al. 2006, Gaillard et al. 2010) and provides the conceptual underpinning for the definition of habitat quality used in this chapter.

As the density of birds in a habitat increases, competition intensifies and diminishes the average fitness conferred upon the occupants (Gaillard et al. 2010; see Consequences of Habitat to Bird Populations, below, for details on how this happens). Thus, theoreticians distinguish the quality of habitat in the absence of interactions with other organisms, called **fundamental habitat quality**, from the quality actually experienced by interacting occupants, called **realized habitat quality**. This distinction allows a more careful examination of how a bird should select among available habitats to maximize its fitness.

Habitat Selection Theory

Human activity fundamentally alters the Earth. Our needs for food, fiber, and energy drive global habitat loss, and yet,

we also have the capacity to engage in targeted conservation (Vitousek et al. 1997, Hoekstra et al. 2005, Steffen et al. 2011). Habitat is paramount to bird conservation; therefore, to balance bird conservation and human needs, we must understand the nuances of “habitat selection”—the study of where birds live and why. Habitat selection is a process that operates at the level of an individual bird (Krebs 2001). Two kinds of factors should be kept in mind when examining habitat selection in birds: (1) evolutionary (or ultimate) factors, which confer fitness consequences on habitat selection; and (2) behavioral (or proximate) factors, which describe the mechanism by which birds select some habitats over others (Krebs 2001).

Wiens (1985) provided a conceptual model to clarify the myriad variables that can affect avian habitat selection (fig. 18.4). A “habitat selection template” represents habitat preferences in a bird that result from both an individual’s genetic makeup and learned preferences through experience (Sogge and Marshall 2000). For example, Klopfer (1963)

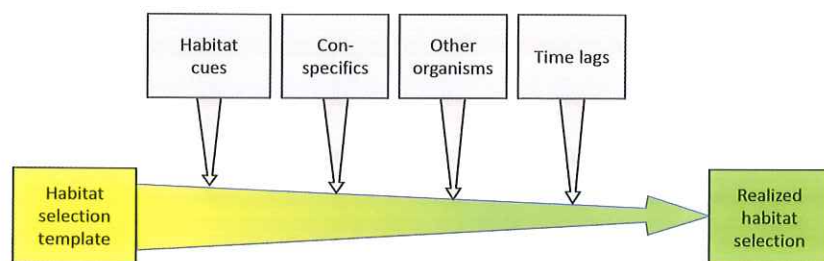


Figure 18.4. A conceptual model of the factors that may affect habitat selection at the local level. These constraints operate to limit the range of habitats occupied by a species. Modified from Wiens 1985.

found that Chipping Sparrows (*Spizella passerina*) experimentally raised in the laboratory selected habitats containing pine branches rather than alternative sites containing oak branches, just as they do in the wild. However, birds raised in the laboratory with oak branches showed diminished selection of pine branches as adults, suggesting a genetic preference for pine could be modified by earlier experience (Krebs 2001). Realized habitat selection, describing what a bird actually selects, is modified from this habitat template by a series of other factors. The cues used by birds are habitat characteristics such as nest sites, cover, food supply, or predation risk that birds can use to make settlement decisions. Habitat selection results if the sum of stimuli from each of these factors exceeds a selection threshold (Cody 1985), which could be raised or lowered depending on the urgency for selection. For example, a migrating bird with depleted fat reserves may be far less picky in selecting habitats than a bird with large stores of fat. The lean bird's low selection threshold may prompt it to select a foraging patch with abundant food even if it poses risk of predation, whereas the fat bird may keep searching for something better (Hildén 1965).

Conspecifics

The presence of conspecifics (i.e., members of the same species) is one of the most important influences on habitat selection. In some cases, low population densities can decrease fitness, and the presence of conspecifics can actually favor habitat selection (see review of so-called Allee effects and other process operating at low density in Stephens and Sutherland 1999, Greene and Stamps 2001). For example, birds may benefit by joining a flock with shared vigilance and a reduced predation risk (Elgar 1989), or they may enjoy greater reproductive opportunities at high density because of improved mate choices (Stephens and Sutherland 1999). Also, a high density of conspecifics can be attractive to an individual if conspecifics are useful cues for resources insensitive to density-dependent competition (see reviews in Stamps 1991, Doligez et al. 2004, Valone 2007). Understanding these processes is important for conservationists, because habitat restoration often operates with a “if you build it, they will come” assumption. This assumption is invalid if a spe-

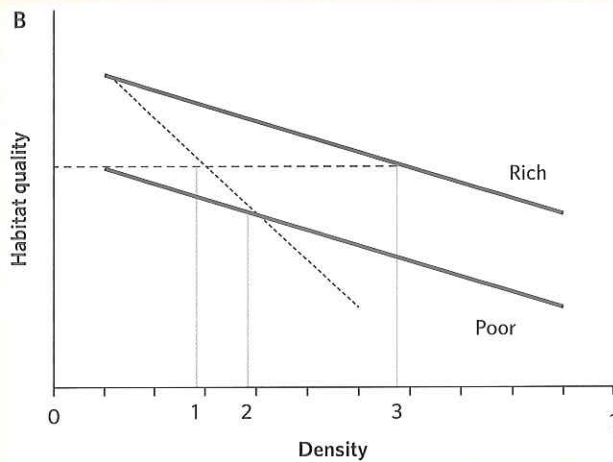
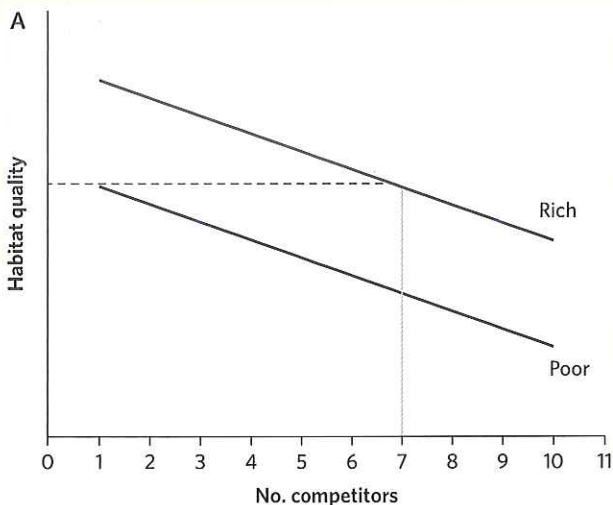
cies is reliant on conspecific attraction for habitat selection (Ahlering and Faaborg 2006). In these cases, simulating the presence of conspecifics can be an important conservation practice. For example, Black-capped Vireos (*Vireo atricapilla*), a bird endangered by loss of habitat and nest parasitism, have been successfully attracted to managed oak woodlands with playbacks of songs and calls (Ward and Schlossberg 2004). Likewise, Common Murres (*Uria aalge*) have been attracted to offshore breeding rocks with decoys of nesting birds, facilitating their return to historic breeding habitats after recovering from long-term population declines (Parker et al. 2007).

More commonly, conspecifics are competitors for limited resources, such as food or nest sites. Assuming that a bird should select the habitat that best increases its fitness, and that competition varies with density of conspecifics, we expect habitat selection to be also density-dependent (Rosenzweig 1981, Morris 1989, Gaillard et al. 2010). Under density-dependence, birds experience realized habitat quality affected by competition with conspecifics, and they choose habitats accordingly (box on page 585). If competitors are equal, this leads to an “ideal free distribution” (IFD; Fretwell and Lucas 1970), in which individuals are distributed among habitats that vary in fundamental habitat quality (also called intrinsic habitat quality or zero-density suitability, sensu Bernstein et al. 1991) such that all individuals experience the same realized habitat quality. In contrast, an “ideal despotic distribution” (IDD) emerges if individuals are unequal competitors, in which the preemption of resources or territories in the highest quality habitats ensures that the strongest competitors reap the greatest rewards (Parker and Sutherland 1986). In this case, at equilibrium the average fitness conferred by a habitat on its occupants—realized habitat quality—is lower in habitats with low fundamental habitat quality (box on page 585).

While the ideal free and ideal despotic models offer great heuristic value, they represent idealized abstractions that usually fail to account for observed distributions of animals (Tregenza 1995, Gaillard et al. 2010). Indeed, wild birds are not omniscient, not free to settle anywhere, and they generally face marked environmental stochasticity that can

IDEAL FREE AND IDEAL DESPOTIC DISTRIBUTIONS

Models of ideal free (A) and ideal despotic distributions (B) (from Fretwell and Lucas 1970, Parker and Sutherland 1986, Bernstein et al. 1991). Two habitats varying in quality are modeled, each showing a linear density-dependent decline in quality. Fundamental habitat quality is the "intrinsic" quality of a habitat in the absence of intraspecific competition; realized habitat quality accounts for negative effects of competition. In the ideal free distribution, the first six competitors select the rich habitat to maximize realized habitat quality conferred; the seventh chooses between the partially filled rich habitat and the empty poor habitat,



which offer the same realized habitat quality at densities of 7 and 1, respectively (depicted by horizontal dashed line). In the despotic distribution model, competitors are unequal. As density increases, weak competitors (heavy dashed line) suffer a steeper decline in realized habitat quality than do strong competitors. At density 1 in the rich habitat, strong competitors occupy the rich habitat only, but for weak competitors, realized habitat quality in the rich habitat has diminished to the level of fundamental habitat quality in the poor habitat. At density 2, it pays weak competitors to occupy the poor habitat exclusively. Strong competitors should not use the poor habitat until they reach density 3. From Johnson 2007.

change the relative value of habitat or prevent expected fitness from being realized (Gaillard et al. 2010). Therefore, there are numerous scenarios that can lead birds to select poor habitats and avoid rich ones (Rapport 1991, Railsback et al. 2003), including incomplete information (Shochat et al. 2002, Stamps et al. 2005), ecological traps (Battin 2004), time lags (Davis and Stamps 2004), a lack of high-quality habitat (Halpern et al. 2005), and others (Bernstein et al. 1991, Block and Brennan 1993, Kristan 2003), some of which we discuss in more detail later. Nonetheless, the distinction between the theoretical Fretwell-Lucas models is important because it reveals opposing prioritizations of habitats for managers. Under the ideal free model, fundamental habitat quality corresponds with density. Therefore, although all individuals receive the same reward at equilibrium, the habitats with the most birds are fundamentally highest in quality and should be prioritized for conservation. This convenience al-

lows managers to simply count birds in different habitats and rank conservation priorities accordingly. Under a despotic distribution, the equilibrium density among fundamentally rich and poor habitats depends on the relative competitive abilities of strong and weak competitors. If weak competitors are much more influenced by competition than are strong competitors, the density of birds in poor habitats is likely to be higher than in rich habitats (Bernstein et al. 1991). In this case, density will be a misleading indicator of habitat quality as cautioned by Van Horne (1983), and prioritizing habitats should involve measuring individual birds' performance to assess variation in realized habitat quality. Thus, it behooves ornithologists to consider whether their study species are more likely to approximate an ideal free or despotic model by carefully considering the likelihood of strong variation in the competitive ability of individual birds owing to differences in age, sex, experience, or knowledge of the habitats.

Other Organisms

As with conspecifics, individuals of other species can contribute either positively or negatively to habitat selection. The presence and abundance of heterospecifics may introduce interspecific competition that could diminish available resources, reduce habitat quality, and discourage habitat selection. Experimental removals of heterospecifics have confirmed their negative influence on habitat selection by showing an expansion into previously unselected habitats (Sherry and Holmes 1988) or an increase in realized habitat quality (Connell 1983). For example when Martin and Martin (2001) experimentally removed Orange-crowned Warblers (*Oreothlypis celata*) from territories in Arizona, Virginia's Warblers (*Oreothlypis virginiae*) shifted their nest locations to sites indistinguishable from Orange-crowned Warbler nest sites, increased feeding rates during both the incubation and nestling periods, and enjoyed reduced nest predation rates, compared with control plots where Orange-crowned Warblers were present. The presence of predator species can also affect habitat selection. It has long been recognized that females select nest sites, in part, to minimize risk of predation (Forstmeier and Weiss 2004), but evidence also indicates that nest predators affect larger scale habitat selection (e.g., selection of territories or habitat patches). For example, Fontaine and Martin (2006) found that birds nested in higher densities in habitats from which rodent nest predators were experimentally removed. Predation also affects habitat selection of nonbreeding birds, as evidenced by studies of Bramblings (*Fringilla montifringilla*) and Western Sandpipers (*Calidris mauri*) that each show avoidance of areas with high risk of predation despite high food availability (Lindstrom 1990, Ydenberg et al. 2004). Fewer examples exist of habitat selection being influenced by parasitic species, but Forsman and Martin (2009) found evidence for selection of parasite-free space by hosts of the parasitic Brown-headed Cowbirds (*Molothrus ater*). There is also evidence that the geographic distribution of some shorebirds (a consequence of evolutionary habitat selection) is in part influenced by exposure to mosquitoes and the diseases they can transmit to birds (e.g., avian malaria; Mendes et al. 2005).

Negative effects of other species on a bird's selection of habitat may be the most obvious, but an accumulating number of empirical studies demonstrate that the presence of heterospecifics, like conspecifics, can provide information about habitat that is useful to birds in their selection of breeding sites (e.g., Doligez et al. 2004, Kivelä et al. 2014). For example, working on an island in the Baltic Sea, Forsman et al. (2009) found that the arriving migratory insectivorous birds showed selection for habitats with high densities

of nonmigratory titmice (*Parus* spp.). In theory, the use of social information (from conspecifics and/or heterospecifics) should persist if the benefits outweigh the costs associated with selecting sites with competitors. More specifically, social information may pay if the environment is too variable for innate habitat preferences to reliably direct birds to high-quality habitats, but sufficiently predictable in time or space for observations of other birds to hold value later (Boulinier and Danchin 1997, Mönkkönen and Reunanen 1999, Doligez et al. 2003, Fletcher 2006, Seppanen et al. 2007).

Time Lags

Time lags in habitat selection result from a delay in a bird's response to changing environmental conditions (Wiens 1985). A common form of a time lag in habitat selection is site fidelity—the tendency to stay in or return to a previously used site or territory (Switzer 1993). The evolution of adaptive time lags is positively associated with homogeneity in territory quality, predictability of territory quality, short life spans, the cost of changing territories, and the probability of mortality in a habitat. However, many bird species show facultative or conditional site fidelity depending on previous nest success. For example, Dow and Fredga (1983) found that female Common Goldeneyes (*Bucephala clangula*) tend to return to sites in which they were previously successful, while they are likely to disperse after a failed nesting attempt. Changes to habitats introduced by human activity are evolutionarily novel, and some species' previously adaptive time lags may render site fidelity maladaptive under current conditions. For example, Walker et al. (2007) found that Greater Sage Grouse (*Centrocercus urophasianus*) leks disappeared from traditionally used sites following coal-bed natural gas development in Wyoming, but not until after an average of about four years. Likewise, Meyer et al. (2002) found that Marbled Murrelets (*Brachyramphus marmoratus*) took several years to abandon nesting sites in old-growth redwood forests after they were fragmented by ongoing harvesting of second-growth forests. A time lag can also delay a bird's selection of habitat that has improved because of human-caused habitat restoration, which can prompt the need for conservationists to overwhelm this time lag to encourage colonization (Ahlering et al. 2010), as described earlier for Black-capped Vireos and Common Murres.

For highly mobile organisms inhabiting dynamic environments, temporal and spatial scales can strongly affect patterns of habitat selection (Hildén 1965). For example, female Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) select marshes based on the emergence of their aquatic insect prey, but they use vegetation density rather than food availability to select individual nesting locations (Orians and

Wittenberger 1991). In this system, prey availability can be forecasted accurately only at a coarse spatial scale, whereas vegetation density varies at a fine spatial scale and is more temporally stable. Thus, at the time of settling, the birds assess information about prey availability and vegetation at different spatial scales in correspondence to their temporal reliability. Indeed, gathering information about the environment is an important determinant of a bird's fitness (Dall et al. 2005), and there is growing empirical evidence that birds sample various habitats ("prospecting") before selecting (Reed et al. 1999, Kristan 2006). Birds selecting habitat in a dynamic landscape face a complex forecasting problem, in that they must choose a location with previous or current information that may not always predict later realized habitat quality (Gates and Gysel 1978, Best 1986, Misenhelter and Rotenberry 2000).

Hierarchical Habitat Selection

All organisms face restrictions in the information they can gather about their environment (Levin 1992), and the interaction between spatial scale and the ability to distinguish features at a distance create different habitat selection processes depending on whether a bird samples primarily at ground level or high above it (Kristan 2003). "Top-down" habitat choice is a hierarchical, sequential process, beginning with a bird flying over a landscape and deciding where to settle based on the habitat encountered (Hutto 1985). In this case, birds are best able to resolve coarse habitat variation, such as landscape features and general types of vegetation, before descending into a location, where they are better able to resolve finer variation, such as foraging sites in different species of trees (fig. 18.5). In contrast, a dispersing juvenile of

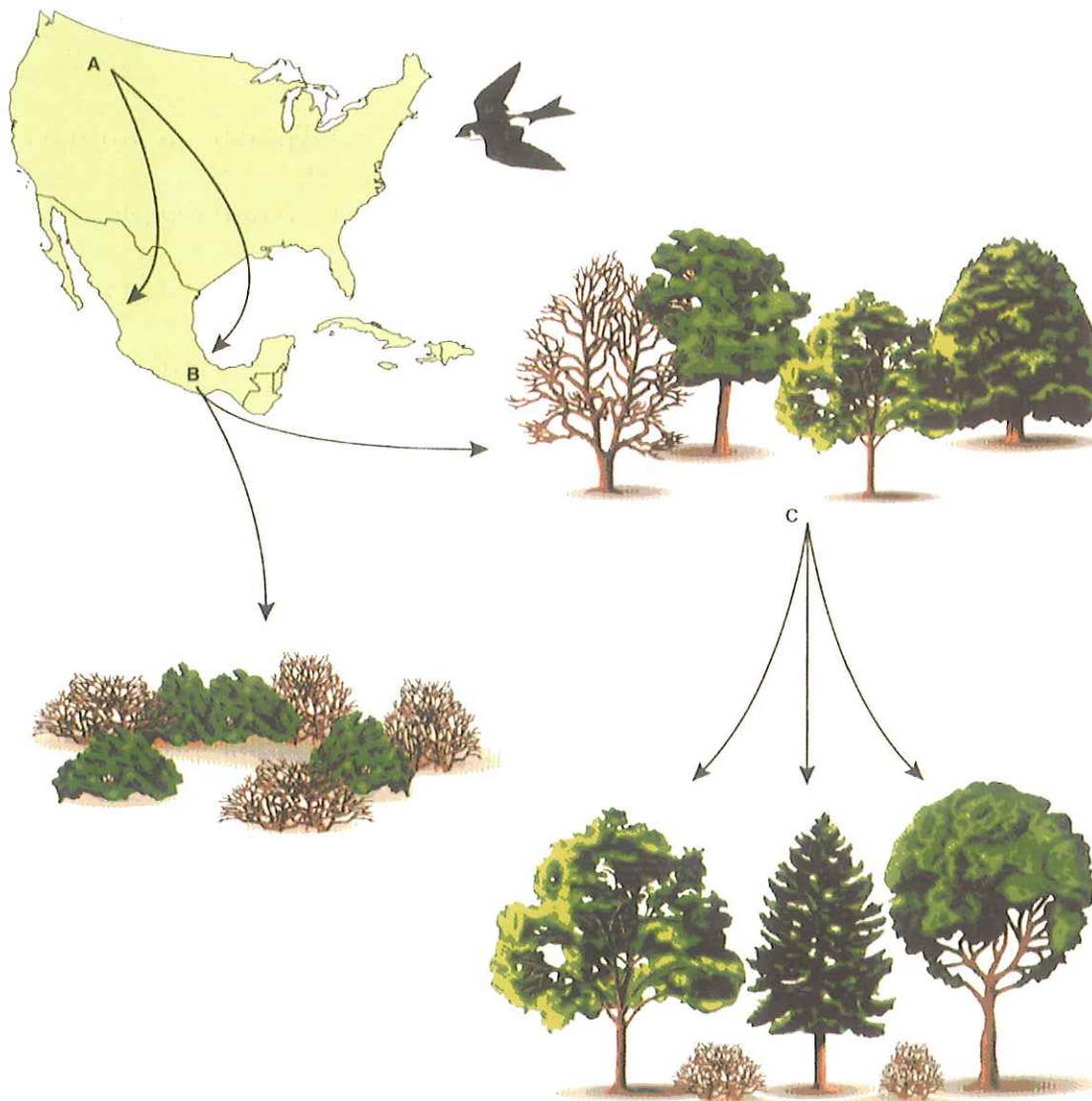


Figure 18.5. Hierarchical decision-making process for the choice of nonbreeding habitat by a migrating Violet-green Swallow (*Tachycineta thalassina*) in Mexico. At A, the bird selects whether to go to southern or western Mexico to overwinter. At B, it selects woodland or shrubland-dominated vegetation. And at C, it selects which of several treetops to occupy. Modified from Hutto 1985; image from Krebs 2001.

a nonmigratory species may move from tree to tree, habitat patch to habitat patch, and sample habitat at a variety of scales simultaneously (“bottom-up” habitat selection). This pattern of movement presents an “information barrier” (Forbes and Kaiser 1994), meaning that a bird lacks knowledge of habitat beyond what it has yet experienced. In these cases, a bird must balance the benefit of sampling distant habitats against the cost of movement, which may be particularly high for juvenile birds. Bottom-up selection may also be favored if local conditions are more consequential than those at larger spatial scales, such as woodpeckers selecting nesting trees within a forested landscape (Lawler and Edwards 2006). In either top-down or bottom-up habitat selection, the optimal habitat may go unused if it is not found (Kristan 2006). Thus, the constraints imposed by incomplete information available to birds at different spatial scales introduce another mechanism by which habitat selection may not follow the “ideal” models, leading birds to make maladaptive choices.

Consequences of Habitat to Bird Populations

It is widely recognized that spatial variation in habitat is central to the regulation of bird populations. This notion is based on two generally accepted tenets rooted in the theory of habitat quality and selection (Newton 1998). First, for any species, habitat varies in quality from place to place and, second, that as a bird’s population size increases, individuals will select good habitat over poor ones. If these conditions hold, then it is inevitable that as population size increases, an increasing proportion of individuals will be pushed down the habitat gradient to poorer habitats where, by definition, their reproduction or survival is diminished (Rodenhouse et al. 1997, Newton 1998). Therefore, the average reproduction or survival will decline overall with increasing density, and rise again when population size is low. This habitat-mediated density-dependence is the essence of population regulation imposed by the quantity and quality of habitats available to birds. Empirical evidence for this pattern is widespread, especially for breeding birds. For example, Peregrine Falcons (*Falco peregrinus*, Mearns and Newton 1988) and Black-legged Kittiwakes (*Rissa tridactyla*, Coulson 1968), which both recovered from historically low population sizes, saw mean reproductive declines with increased population size. Similarly, Black-throated Blue Warblers (*Setophaga caerulescens*, Rodenhouse et al. 2003) and Tengmalm’s Owls (*Aegolius fumereus*, Korpimäki 1988) had increased breeding performance with lower population size. For more details of avian population ecology, see chapter 21.

Sources, Sinks, and Traps

Survival and reproduction in especially poor habitats may be insufficient to maintain local populations; thus poor habitats

act as “sinks” in the landscape. The persistence of sinks on the landscape is thus reliant on emigration from other better habitats, acting as “sources” of surplus birds. This source-sink model is an enduring one in habitat ecology (Pulliam 1988, Pulliam et al. 1991), and has prompted other advances in our understanding of the roles of habitat selection and quality in animal population dynamics. For example, while birds appear to generally distinguish habitat quality well enough to show selection for sources over sinks, in some cases this is not so. These attractive sinks are called “ecological traps.” Theory suggests that, under most circumstances, their presence in a landscape will drive a population to extinction, prompting an urgent need for conservationists to identify them and manage accordingly (Kristan 2003). Typical population modeling does not consider habitat selection explicitly and may mask the effects of ecological traps, leading to overly optimistic predictions about population persistence (Battin 2004). Ecological traps may arise if human-caused changes in the habitat decouple the habitat cues birds use to select habitat from the characteristics that afford realized habitat quality. Evolution may be too slow for birds to respond immediately to these human-caused changes, trapping birds into selecting bad habitats. Specifically, habitat alteration capable of creating an ecological trap must either alter the cues birds use to select habitats (increasing their attractiveness), sharply decrease the quality of a habitat associated with cues, or both (Robertson and Hutto 2006). For example, Weldon and Haddad (2005) found that Indigo Buntings (*Passerina cyanea*) actively selected edgy patches of habitat in South Carolina, where they suffered high rates of predation, presumably because the human-created edges created (evolutionarily recent) were highly attractive to nest predators (Weldon 2006, fig. 18.6).

Habitat Distribution

It is not just the quality and quantity of habitats that affect population dynamics of birds; it is also the spatial distribution of habitats in a landscape (Newton 1998). The distribution of some habitats, such as mountaintops and aquatic habitats are naturally patchy, but relentless human activity has fragmented other once-continuous habitats into small patches embedded in a matrix of land modified for people to grow crops, harvest other resources, and live, work, and play (Perfecto et al. 2009). Indeed, up to 40 percent of the Earth’s ice-free terrestrial land surface is devoted to agriculture, 20 percent to managed forests, and almost 10 percent to human settlements, with only about 10 percent in protected areas (Foley et al. 2005). Thus, most bird species live in a mosaic of disturbed and (comparatively) undisturbed habitat patches. For many species, the individuals inhabiting

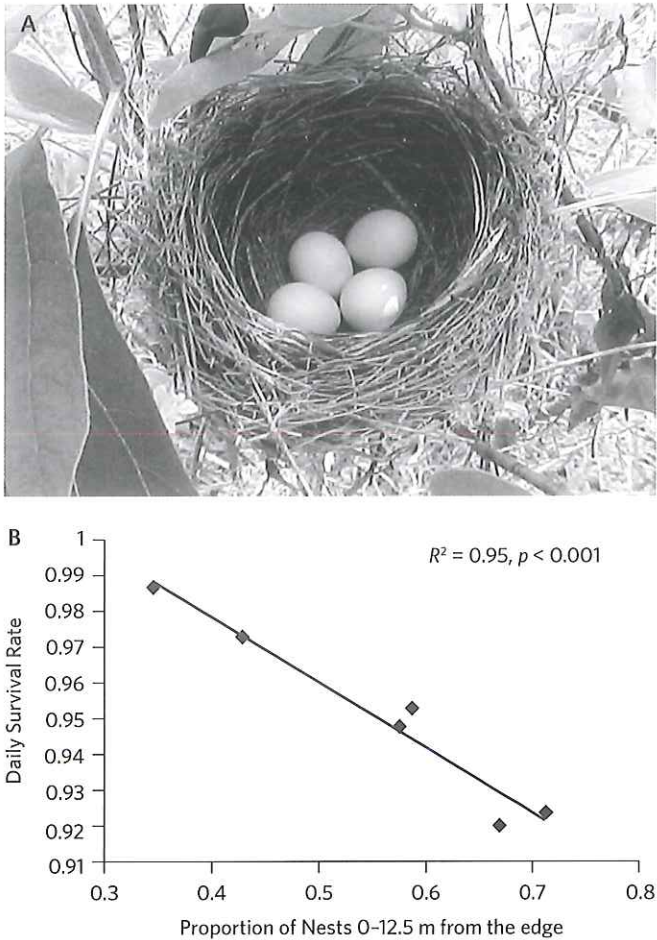


Figure 18.6. A, Indigo Bunting nest. From Weldon and Haddad 2005; photo by A. Weldon. B, Daily survival rates of Indigo Buntings declined as a function of the proportion of nests 0–12.5 m from the edge across nesting periods and treatments. From Weldon 2006.

these patches may interact as “subpopulations,” and the collection of them all, called a “metapopulation,” may persist or fail following processes that transcend the fates of bird in individual patches (for further details of metapopulations, see chapters 20 and 21). Specifically, the extinction risk for a metapopulation depends on the balance between the loss of subpopulations because of local extinction and the gain (or regain) of subpopulations because of (re)colonization. For a given ensemble of subpopulations, an equilibrium exists in which loss and gain rates are equal, resulting in persistence of the metapopulation, even while individual subpopulations may blink in and out of existence. This equilibrium depends on the rate of movement among habitat patches, and the per-patch rate of local extinction (Kareiva and Marvier 2015). That local extinctions in patches (fragments) are a normal and inevitable part of ecosystem dynamics is now rarely questioned by ecologists (Perfecto et al. 2009). For example,

long-term experiments in Amazonian forests show that bird extinction rates are surprisingly high in even the largest patches of forest, underscoring the importance of movement among patches to ensure metapopulation persistence (Ferraz et al. 2003). Metapopulation theory is therefore probably generally appropriate for many bird species, but it suffers from an implicit assumption that the matrix between patches is homogeneous and comparatively poor in quality. A growing body of research, sometimes called countryside biogeography, challenges this assumption (Mendenhall et al. 2014). This work places more focus on understanding how variable habitat conditions in the matrix contribute to metapopulation persistence by either supporting birds outside conventionally “intact” habitat patches or by improving the permeability of the matrix and enabling birds to move among habitat patches more successfully (Perfecto et al. 2009).

Habitat Complementarity

While metapopulation theory prompted ecologists to recognize the importance of habitat distribution in a landscape, the idea of habitat complementarity emphasizes how the distribution of different habitats sometimes matters to birds at much finer scales as well. This notion applies to bird species that require markedly different habitat attributes within a single phase of their annual cycle (Dunning et al. 1992). For example, breeding Ruffed Grouse (*Bonasa umbellus*) require unique habitats for their drumming mating displays (conifer forest with fallen logs), nesting sites (high shrub density to help conceal nests), and brooding habitats where chicks are reared (abundant forbs and insects as food supply). These must be arranged in close proximity to enable birds to complete their breeding cycle (Gullion 1988). A similar story applies to Northern Spotted Owls in California, which achieve higher per capita fitness potential in territories that are composed of a mixture of old forests for nesting sites and other forest types that harbor abundant rodent prey (Franklin et al. 2000; fig. 18.3).

Seasonal Shifts and Migratory Species

The consequences of using different habitats at different times are most pronounced for migratory birds. For example, many birds that breed in mature deciduous forests, such as the Wood Thrush (*Hylocichla mustelina*), shift to using shrubby habitats after young have fledged (Vitz and Rodewald 2006). These changes are likely caused by shifting resources and constraints over time. For example, the availability of protein-rich food such as insect larvae is especially important during the breeding season to foster nestling growth (Greenberg 1995), whereas dense cover and abundant fruit resources increase in importance after breeding so that birds can better

avoid predation and fuel their oncoming migrations (Vitz and Rodewald 2007, 2011). The complexities of habitat requirements over the annual cycle peak with long-distance migrants, such as those that breed in north temperate forests and migrate back and forth from tropical nonbreeding habitats. Although breeding habitats profoundly affect populations, nonbreeding habitat can be at least as important (Rodewald 2015). Sillett and Holmes (2002) showed that 85 percent of mortality of Black-throated Blue Warblers occurred during the migratory period, underscoring the imperative to protect habitat used by migrant birds en route between their breeding and nonbreeding ranges (Moore and Barrow 2000). Moreover, changes in population size in one season can affect density-dependent processes in another (Marra et al. 2015a), meaning the habitat that a bird selects in the breeding season can “carry over” and affect its nonbreeding survival, or vice versa (Norris et al. 2004, Marra et al. 2015b). For example, American Redstarts (*Setophaga ruticilla*) that overwinter in high quality mangrove forests arrive on the breeding grounds earlier, in better condition, and fledge more young than do birds that overwinter in lower quality scrubby habitats with a less reliable food supply (Marra et al. 1998, Norris et al. 2004, Cooper et al. 2015). These processes have been most studied in birds with conspicuous global migrations, but they likely occur for many bird species, and ornithologists must remain attentive to the role of habitat in bird populations throughout the annual cycle (Marra et al. 2015a; box on page 590).

MEASUREMENTS IN HABITAT ECOLOGY

The previous sections underscored the imperative for avian ecologists to understand habitat use, selection, and quality for birds throughout the annual cycle, which of course demands we accurately measure habitats and document how birds use and select them. In this section, we first review methods of measuring habitats, both remotely and on the ground, then provide an overview of current methods for quantifying habitat use, selection, and quality for birds in the field. A persistent theme throughout this section is that new technologies can be harnessed by ornithologists to help measure habitat in ways that advance our understanding of birds and how to conserve them.

Measuring Habitat Attributes

When it comes to measuring habitats, the critical challenge facing ornithologists is to determine which habitat attributes to measure and how to accurately quantify them. The traditional approach has been to measure habitat attributes at ground-based locations (e.g., breeding bird territory) and

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Seabirds inhabit vast ocean basins, and their distributions and populations are influenced by the effects of basin-wide oceanographic processes, such as the El Niño/La Niña phenomena, on marine food availability. In contrast, local processes, such as the invasion of nesting islands by introduced predators or disturbance of nesting colonies, can also strongly affect seabirds, causing numerous extinctions and threatening many more. Thus, understanding seabirds and their conservation can require detailed knowledge of processes that occur at both of these levels.

Seabird ecologist Enriqueta Velarde, senior researcher at Universidad Veracruzana in Xalapa, Mexico, reveals how both region-wide and local processes affect seabirds, and how to use such information to conserve seabirds. Dr. Velarde has worked for almost 40 years on Isla Rasa in the Gulf of California, and during this time has essentially prevented the extinction of not one but two seabird species that principally nest there: Heermann's Gull (*Larus heermanni*) and Elegant Tern (*Thalasseus elegans*). Beginning in the early 1980s, Velarde and colleague Jesús Ramírez worked tirelessly to reduce human disturbance at Isla Rasa, followed by a campaign in the early 1990s to remove introduced rats and mice on the island. The success of these efforts not only secured the future of Heermann's Gull and Elegant Tern, but inspired a larger effort to conserve numerous island endemic taxa using the same techniques at a much larger scale, directly resulting in tangible conservation impacts.

Beyond preventing extinctions and inspiring a generation of conservation biologists, Velarde's work on the diet of seabirds nesting on Isla Rasa has shown how shifts in diet are a harbinger of oceanic changes to come. In El Niño years, the diets of Heermann's Gull, Elegant Tern, and California Brown Pelicans (*Pelecanus occidentalis californicus*) shift markedly from Pacific Sardine to Northern Anchovy, while in La Niña years, the converse occurs. These shifts impressively predict the success of the Gulf of California's sardine fisheries in the following year. Such information helps further understanding of large-scale oceanic processes and efforts to manage Gulf of California fisheries. The seabirds of Isla Rasa thus forecast change to come in a way that benefits humans—and Dr. Velarde first prevented their extinction and then showed us how we can learn something unique from them about their difficult-to-study marine habitats.

then statistically relate these findings to bird habitat use, selection, and quality (Morrison et al. 2012; see below for more details and additional references).

For decades, ornithologists have recognized that broad-scale habitat features are important drivers of bird distribution patterns and avian community organization. The distribution of many avian species mirrors the distribution of their habitats. Sometimes distributions are determined by the juxtaposition of multiple habitat types required during different life stages. For example, Golden-winged Warblers (*Vermivora chrysoptera*), a species of conservation concern, require early successional shrubby habitat for breeding throughout eastern and midwestern forests. However, recent work indicates that early successional habitats that are critical for nesting must be surrounded by dense forests necessary for foraging adults (Streby et al. 2012). If habitat attributes were not quantified at larger areas than the breeding territory, the importance of dense forest to breeding Golden-winged Warblers may have gone unrecognized. Therefore, ornithologists acknowledge that habitats should be quantified at multiple spatial extents (e.g., breeding locations and areas surrounding breeding sites). This idea requires considerable effort and, in many cases, is impossible to achieve using traditional on-the-ground measurements. To circumvent this challenge, ornithologists have increasingly adopted the use of data collected from remote sources (e.g., Palmeirim 1988, Gauthreaux-Jr. and Belser 2003, Gottschalk et al. 2005, Vierling et al. 2008). Linking habitat data on the ground with data from remotely

sensed measurements can enhance our ability to characterize avian habitat across large areas. This allows for a more complete understanding of habitat quality and its relation to bird demographics and distributional patterns than is possible with data from a single scale (Wiens and Rotenberry 1981, Saab 1999, Wood et al. 2016). It is critical to understand avian habitat quality and selection at multiple spatial scales. A spatial scale is a combination of extent (i.e., the area of habitat under study) and grain (i.e., the resolution at which a habitat is studied). Many species of birds select habitat hierarchically (see Hutto 1985 above), and therefore, understanding habitat quality and selection at multiple spatial scales underscores the importance of “landscape ecology” (i.e., study of ecological processes in the environment, Turner 1989) in ornithology.

Below, we provide a more in-depth overview of the ways in which ornithologists measure habitat on the ground and from remote data sources. We describe case studies and also detail a handful of advances in bird-habitat quantification that will likely aid our understanding of bird demographic and distribution patterns throughout the annual cycle. On the ground measurements (**ground-based measurements**) provide a fine-resolution overview of the immediate habitat that a bird experiences: the structure of vegetation, the diversity of plant species and food resources, and the presence of other species, such as predators, competitors, mutualists, and commensalists (Morrison et al. 2012), all of which influence habitat selection patterns by birds (Cody 1985). Once habitat attributes are measured during fieldwork, those data

Table 18.1. Examples of techniques that can be used by ornithologists for measuring territory-level habitat attributes that may influence breeding bird species habitat selection.

<i>Habitat attributes</i>	<i>Reference</i>	<i>Technique</i>
<i>Vegetation structure</i>		
Cover classes	Martin et al. 1997	Circular plot
Vegetation density	James 1971	Circular plot
Vertical vegetation structure	MacArthur and MacArthur 1961, Robel et al. 1970	Point sampling
Horizontal vegetation structure	Nudds 1977	Cover board
<i>Vegetation composition</i>		
Tree diversity	Mitchell 2001	Point center quarter
Species lists	Wood et al. 2011	Relevé
<i>Food availability</i>		
Insects	Cooper and Whitmore 1990, Johnson 2000	Branch clipping
Fruits and nuts	Koenig et al. 1994, Higgins et al. 2012	Seed traps and visual counts
<i>Predators and Conspecifics</i>	Ralph et al. 1995	Point counting

Table 18.2. Examples of remote sensing data and techniques that can be used by ornithologists for measuring habitat attributes that may influence breeding bird species habitat selection.

Remotely sensed habitat features	Reference	Data or Technique
<i>Passive remote sensing</i>		
Land cover	Homer et al. 2015	Land cover data
Habitat loss and fragmentation	Briant et al. 2010	MODIS
Habitat phenology	Toral et al. 2011	Landsat
Vegetation structure	Wood et al. 2012	Aerial photographs
Vegetation composition	Martin et al. 1998	Airborne hyperspectral data
<i>Active remote sensing</i>		
Vegetation Structure	Bergen et al. 2009	LIDAR and RADAR

are then commonly linked via statistical modeling to bird demographic and distributional patterns (Morrison et al. 2012). The traditional approach has been to define a sampling unit within some area of interest, be it a habitat patch, survey plot, or individual territory. The sampling unit is often centered on a bird survey location (e.g., a point count or a nest site), and information is collected regarding habitat attributes known or hypothesized to be relevant to the species (see table 18.1 for some common examples). Excellent reviews of techniques for measuring vegetation, prey availability, fruit and seed abundance, and other biotic and abiotic attributes of habitat relevant to birds are provided by Cooperrider et al. (1986) and Higgins et al. (2012). An overview of common approaches to surveying birds and their habitats is provided in chapter 31.

Remote Measurements

More recently, with the advent of technology and the emergence of the field of landscape ecology, ornithologists have adopted the use of data from remote sensing for characterizing habitat attributes at broad spatial and temporal extents. There are two typical approaches for using data from remote sensing: passive and active remote sensing (table 18.2). Here, we provide an overview of remote sensing approaches used by ornithologists. For further reading on the importance of remote sensing in biodiversity studies, see the excellent reviews by Nagendra (2001), Kerr and Ostrovsky (2003), Turner et al. (2003), Bradbury et al. (2005), Gillespie et al. (2008), and Pettorelli et al. (2014).

Passive Passive remote sensing involves the use of sensors that measure the reflectance of natural radiation (e.g., reflected sunlight) by the Earth (Turner et al. 2003). The

most common forms of these data are from aerial photography and satellite imagery (Turner et al. 2003, Pettorelli et al. 2014). Aerial photographs are generally acquired from cameras mounted on airplanes (Morgan et al. 2010) and more recently by unmanned aerial vehicles (i.e., drones, Anderson and Gaston 2013). Aerial photographs are typically very detailed images with resolutions as low as <1m and are extremely useful for mapping fine-grained variability in vegetation across areas as large as the extent of the photographs (Fensham and Fairfax 2002). This is useful for describing habitat attributes important to birds over extents larger than are typically possible with ground-based surveys (Wood et al. 2012). In addition to the high tonal detail, aerial photographs are extremely useful for mapping and monitoring landscape change in regions where aerial photographs have been taken for decades (Morgan et al. 2010). For example, in Oklahoma, researchers were able to characterize woody-plant encroachment (by juniper, *Juniperus* spp.) in grassland habitats, which were then linked to declines in grassland birds (Coppedge et al. 2001). The other common form of passive remote sensing is from satellite imagery, which is used by ornithologists to map landcover and habitat. Typically, satellite images do not provide data at the resolution of aerial photographs (though, as an example, the resolution of the Quickbird Satellite is 0.65 m). Yet, the strength of satellite imagery is in the high temporal replicability of imagery over broad spatial extents. For example, a common satellite data source is derived from the Landsat thematic mapper, which provides multispectral imagery at a 30 m resolution over most of the Earth and has been used by ornithologists for characterizing habitat attributes that are then linked to bird distribution patterns (e.g., Culbert et al. 2012). The Landsat program launched its first earth-monitoring satellite in 1972, and since then, updated satellites have been put into Earth's orbit providing imagery at a given location every 16 days. The combination of relatively high spatial and temporal resolution of Landsat data has allowed ornithologists the opportunity to characterize both long- and short-term changes in habitat, which can be linked to bird distribution patterns (Knick and Rotenberry 2000).

Ecologists use data from passive remote sensing to describe land cover composition, fragmentation patterns, and habitat structure (Turner et al. 2003), and recent advances allow for fine resolution habitat mapping, characterization of vegetation composition, and phenology monitoring (Pettorelli et al. 2014). Traditionally, ecologists have used passive remote sensing to classify vegetation into categories ("vegetation types"), often converting raster-based imagery into polygons circumscribing similar vegetation to create so-called vegetation maps. Raster-based images are composed of pixels (i.e., grid dots), wherein each pixel is composed of

a digital number (e.g., assigned color or black-and-white value). Polygons are vector-based data (i.e., geometric shapes, such as points, lines, or polygons), which ornithologists typically create using geospatial analysis programs to delineate boundaries of habitat patches or study areas. But as we learned earlier, habitat encompasses far more than the vegetation around a bird. So, ornithologists continue to expand the use of data from passive remote sensing sources to provide more nuanced habitat data, which has advanced our understanding of the role of habitat in structuring avian communities, populations, and individuals' habitat selection patterns. For example, "habitat structure"—generally defined as the physical arrangement of vegetation and other habitat attributes in space—is widely recognized to affect birds (Rotenberry 1985) but is time-consuming to measure, and thus is often only accomplished at small scales with on-the-ground field surveys. To address the issue, ornithologists have adapted the use of passive remote sensing approaches to measure habitat structure across broad spatial extents. One promising approach is image texture analysis. Raster-based images, whether satellite images or aerial photographs, are composed of tone, which is the reflectance value (i.e., digital number) of a particular cell. Texture refers to the spatial relationships of tonal values of neighboring pixels, and it is possible to quantify these relationships across an image (Haralick et al. 1973, Haralick 1979). Why texture analysis has proven important to ornithologists is because texture from remotely sensed images, such as air photos or satellite scenes, is correlated with heterogeneity in vegetation and habitat structure (Culbert et al. 2012, Wood et al. 2012, fig. 18.7), and in turn is an excellent predictor of bird species richness (St-Louis et al. 2006, 2009, 2014) and diversity (Wallis et al. 2016), habitat use patterns (Tuttle et al. 2006), habitat suitability (Bellis et al. 2008), and habitat quality (Wood et al. 2013).

Passive remote sensing using satellite imagery can also be useful for deriving measures of other habitat properties, such as net primary productivity and vegetation phenology (timing of plant growth). For example, imagery from several multispectral satellites has been used to calculate the normalized difference vegetation index (NDVI; Gottschalk et al. 2005, Higgins et al. 2012). NDVI is derived from the red to near-infrared reflectance ratio, which provides information about plant structure and growth because chlorophyll absorbs red light, and mesophyll scatters near-infrared light. Numerous multispectral satellites provide data used to calculate NDVI. Landsat data are widely used to calculate NDVI; another satellite platform that has proved valuable to ornithologists is the advanced very-high-resolution radiometer (AVHRR), which has a fairly coarse resolution (≥ 1 km), but a high temporal resolution (1 day). NDVI metrics calculated

using AVHRR data can thus be used to examine temporal changes in primary productivity, green-up, and the length of the growing season, as well as other relevant habitat attributes (Higgins et al. 2012). For example, Sanz et al. (2003) used NDVI metrics calculated using AVHRR data to show that global climate change is causing oak leaf-out to have occurred earlier in the Mediterranean region, and the peak date of caterpillar abundance is advancing accordingly. However, Pied Flycatchers (*Ficedula hypoleuca*) did not change their arrival time between 1980 and 2000, causing a mismatch in peak food supply and the birds' nesting cycle. Determining the broad-scale pattern of oak leaf emergence in relation to caterpillar abundance and Pied Flycatcher arrival at breeding locations would not have been possible without the use of satellite imagery for mapping vegetation change among years.

Active In contrast to passive remote sensing, active remote sensing involves sensors that are mounted with devices that actively emit information such as laser (LiDAR) or motion pulses (RADAR), which are then bounced back to the sensor (Pettorelli et al. 2014). The use of data from active remote sensing platforms has exploded over the past decade, in particular because as remote sensing technology has advanced, active sensing techniques have been developed to gather structural features from below the canopy level (Martinuzzi et al. 2009). The advance of active remote sensing has proved incredibly important for bird-habitat studies, in particular for the ability to map fine-resolution habitat structural features across broad extents, especially during the breeding period, when forested systems typically form a dense canopy of tree cover. Two active remote sensing applications that we will highlight in this chapter are RADAR (Imhoff et al. 1997, Bergen et al. 2009) and LiDAR (Light Detection and Ranging; Bradbury et al. 2005, Vierling et al. 2008).

As described above, active remote sensing procedures have improved our ability to measure habitat attributes beneath the canopy over broad spatial extents. For example, in Wisconsin forests (USA), ornithologists were interested in describing patterns of bird species richness in relation to forest structural attributes. Many of the forest birds of the study area breed in the understory and respond strongly to differences in fine-resolution forest attributes, such as shrub and tree density. The ornithologists were interested in describing bird species richness over a broad spatial extent, and therefore it was necessary to use data from remote sensing sources. However, the forested system was dominated by tall, broad-canopy oak (*Quercus* spp.), hickory (*Carya* spp.), and maple (*Acer* spp.) trees, and passive remote sensing methodologies would not be effective at characterizing forest structure below the canopy. Therefore, the researchers used LiDAR to characterize fine-resolution differences in forest

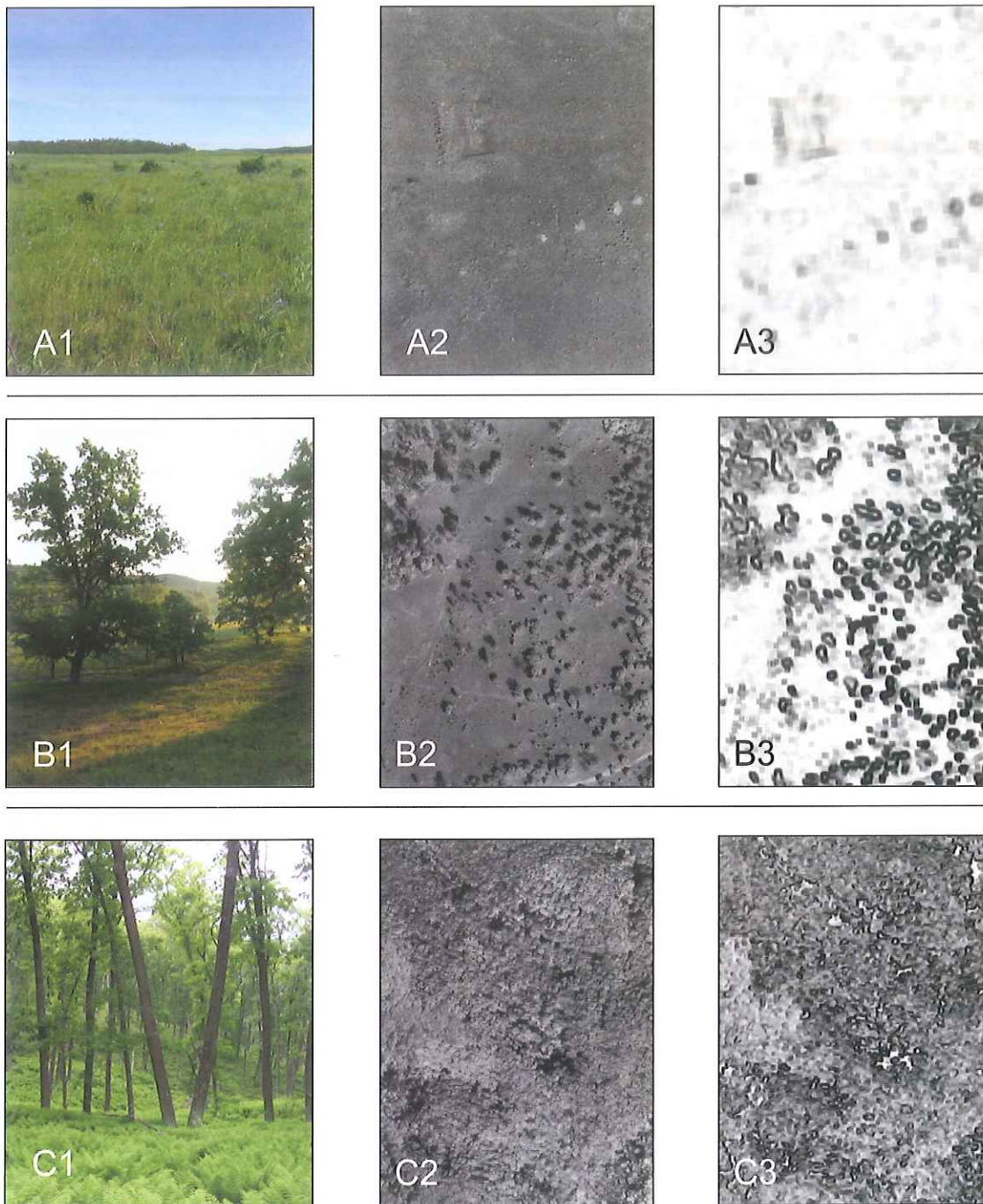


Figure 18.7. Three vegetation types across an open to closed tree canopy continuum: A, Grassland; B, Savanna; C, Woodland at Fort McCoy Installation in Wisconsin, USA. Each vegetation type depicted with (1) a ground photograph, (2) an infrared air-photograph, and (3) an infrared air-photograph processed for first-order variance (image texture).

structure, which were then related to patterns of breeding bird species richness (Lesak et al. 2010). Using a similar rationale to the Wisconsin system (i.e., to characterize understory vegetation structure, which are then linked to bird data), researchers have used LiDAR to describe density of birds in conifer forests of the Black Hills, South Dakota, USA (Clawges et al. 2008); foraging locations by woodpeckers (*Picidae* spp.) in Idaho conifer forests (Vierling et al. 2013); and territory quality for migratory birds in a mixed forest system in central New Hampshire (Goetz et al. 2010).

In addition to the LiDAR studies, ornithologists have used RADAR data to characterize bird habitat at broad spatial extents. For example, in northern Australian eucalyptus (*Myrtaceae* spp.) and melaleuca (*Melaleuceae* spp.) woodlands and forest, Imhoff et al. (1997) used Synthetic Aperture Radar (SAR) in combination with aerial photography to map bird habitat (i.e., vegetation structure). Building on these findings, Bergen et al. (2007) integrated SAR data with optical remote sensing data to describe bird habitat in forest habitats of northern Michigan. Bergen et al. (2007) found that

including RADAR information, which characterized biomass, in their analyses improved habitat classification for forest bird species. LiDAR and RADAR data can capture redundant habitat information (Hyde et al. 2006). Nevertheless, the use of active remote sensing data has greatly improved our ability to characterize bird habitat across broad spatial extents (Bergen et al. 2009). What is next for remote sensing in ornithology habitat research? While this remains a “hot” topic of exploration, the next frontier of passive and active remote sensing will likely involve finer-resolution characterizations of habitat features that can be linked to bird distributions (e.g., discriminating plant species, Roth et al. 2015).

Measuring Habitat Use

Habitat use generally refers to a bird’s use of physical and biological components in a habitat, such as the consumption of food or the occupation of a nest cavity. Habitat use therefore can be directly described from associating the presence of a species with habitat features, or from observations of how animals interact with habitat features (Gaillard et al. 2010). Use of a habitat does not necessarily indicate the conditions that are most preferred by a species, or those that are most strongly associated with fitness. Habitat use, rather, simply reflects what is being used by an individual. Often, to describe habitat use patterns, ecologists typically will measure habitat attributes in areas where birds are observed or where they are engaged in particular behaviors (e.g., foraging). Another approach is to map locations of individual birds marked with unique colored leg bands, which can show how birds use habitats (e.g., Gregory et al. 2004). Likewise, locations of birds obtained from radio (very high frequency, VHF) telemetry can reflect the frequency with which a bird uses different habitats within their home range or territory (Powell 2000).

Technological advances enable ornithologists to measure habitat use in new ways. Locations obtained from global position system (GPS) receivers small enough to be mounted on birds allow more accurate, fine-scaled habitat associations, and thus more realistic estimates of habitat use than some previous techniques (Cagnacci et al. 2010). Other advances in the remote detection of bird locations include the use of increasingly sophisticated remote or bird-borne cameras (O’Connell 2010, Gómez-Laich et al. 2015), telemetry transmitters that communicate with satellites or cell phone networks (Millspaugh et al. 2012), and other animal-borne sensors that can reveal a bird’s location, such as “geolocators” (or global light location sensors) useful for tracking migratory birds too small to carry heavier, more precise technologies (e.g., Hallworth et al. 2015). For additional details on avian movement ecology and remote sensing, see chapters 19 and 31.

Measuring Habitat Selection

Habitat selection is an evolutionary response to a species’ environment, resulting from a complex, hierarchical process of behavioral choices. Johnson (1980) defined habitat use to be selective if components of habitat are used disproportionately to their availability. Availability refers to a component being present and ready for immediate use; it must be accessible or obtainable by a bird (Hall et al. 1997, Gaillard et al. 2010).

Used, Unused, and Available

The methods ornithologists use to measure and infer habitat selection vary in their precision and applicability (Allredge and Ratti 1986, Thomas and Taylor 1990, Jones 2001). Habitat selection is tested for wild birds in two main ways: comparing used habitats with unused habitats and comparing used habitats with available habitats (i.e., randomly-located plots) (Jones 2001). Used habitat is measured as described above. Available habitat refers to all habitat biologically available to a bird in the area of interest. Unused habitat is a subset of available habitat; it is available but reliably documented to not be used by a given species at a given time. For example, consider a cavity-nesting species such as a woodpecker: a tree with an active nest cavity is “used,” trees within the species’ range and large enough for a cavity are “available,” and an “unused” tree is an available tree demonstrably lacking an active nest cavity. By statistically comparing either used vs. unused or used vs. available habitats, researchers can draw inference about habitat selection and avoidance (Manly et al. 2002). Thomas and Taylor (1990) provide a review of several study designs and common statistical techniques for these sorts of approaches.

There are pros and cons for used vs. unused and used vs. available approaches (Manly et al. 2002), and disagreements persist over which is more informative and less subject to violations of statistical assumptions or logical limitation. The reconciliation is far beyond the scope of this chapter, but we highlight a few points to consider when designing studies or interpreting their findings. With used vs. unused approaches, it is often difficult to confirm that a location is truly unused, since the detection probability of birds is rarely 100 percent (MacKenzie et al. 2009). In addition, absence from a particular habitat does not mean that the habitat is being avoided (Wiens 1989), since various constraints, including low population density and dispersal limits, may have a major effect on which habitats are used or not (Pulliam 2000, Jones 2001). Further, a bird’s use of a particular habitat affects its use of other habitats (Thomas and Taylor 1990, Aebischer et al. 1993), and this introduces a lack of independence in data that can negatively affect the power of some statistical techniques (Jones 2001). Nonetheless, only by comparing used and

unused locations can statistical models yield estimates that reflect the true probability a bird uses a given site, a metric enormously useful for managers making land use decisions (Manly et al. 2002). In contrast, used vs. available approaches have advantages but can only yield relative probabilities and indices of selection. Another disadvantage of used vs. available comparisons is that articulation of relevant habitat availability is problematic. For example, researchers routinely remind us that availability refers to both the accessibility and obtainability of resources, not just their abundance (Hall et al. 1997, Jones 2001). Blindly distributing random plots on a landscape (to provide sample units of available habitat) may not reflect true availability, and may result in uninformative results (e.g., a landbird selects terrestrial and avoids aquatic habitats). Johnson (1980) also emphasized the importance of scale and research question specificity in delineating available habitats. He identified four “orders” of habitat selection corresponding roughly to Hutto’s (1985) depiction of top-down hierarchical habitat selection (fig. 18.5). Of course, these levels of selection are only landmarks belonging to a continuum from very fine to very coarse spatial scales (Mayor et al. 2009, Gaillard et al. 2010). With this approach, a researcher might wish to examine how birds select where to place their territory within a larger landscape (Johnson’s “second order” of habitat selection) or how they select specific nest site locations within their home range (Johnson’s “fourth order”), and these questions demand different sets of available habitats for comparison.

Statistical Procedures

In recent years, a growing number of statistical procedures for analyzing habitat selection have been proposed. Two main philosophies can be recognized (Gaillard et al. 2010). The first approach includes methods rooted in ecological niche theory. It typically aims to yield maps of spatial distribution, and it involves analysis of remotely sensed biophysical and habitat variables at used locations in correspondence with random available locations obtained in a geographic information system (GIS). Although this design has been referred to as “presence-only,” analyses still involve comparisons between used and available locations. This approach yields models often labeled species distribution models (SDMs). One of the earliest SDMs involved generalized linear models to predict the distribution of the Rufous Scrub-bird (*Atrichornis rufescens*) using locality records of the species and remotely mapped environmental variables obtained from a GIS (Elith and Leathwick 2009). Much work involving SDMs continues with birds today. Armed with a sample of bird locations and environmental data from a GIS, ornithologists can use specialized modeling procedures (such as MaxEnt; Phillips et al.

2006) to develop predictive maps of bird distribution useful for conservation practitioners and as tools for making predictions of birds’ responses to land use and climate change scenarios (Benning et al. 2002). An almost synonymous approach, usually called ecological niche modeling (ENM, Peterson et al. 1999, Warren and Seifert 2011), tends to place less emphasis on implications for population processes and more on the biophysical variables associated with a species distribution—the fundamental niche of a species (Peterson et al. 2001, Peterson and Soberón 2012). This philosophical approach provides useful and reliable description of the multivariate niche and is often used to map the habitat for a population or species at broader spatial and temporal scales in a manner consistent with the niche-based definition of habitat (Gaillard et al. 2010).

The second philosophical approach emphasizes drawing reliable inference on habitat attributes actively selected by the species studied: that is, testing for habitat selection (Gaillard et al. 2010). Typically, researchers use environmental data to distinguish locations where birds are observed (used locations) from the pool of available locations to reveal habitat selection (see review by Jones 2001), often by using a statistical regression technique (logistic regression or more advanced general linear models) to yield a resource selection function (RSF; Manly et al. 2002). Assuming that the null model of no selection corresponds with a proportional relationship between use and availability, one can statistically test whether a given habitat component is selected for, selected against (aka avoided), or not selected. This philosophical approach emphasizes hypothesis testing and enables quantifying the contribution of individual habitat attributes to a habitat selection (Gaillard et al. 2010). An important variant on this approach compares used and unused locations while explicitly acknowledging imperfect detection probability. Although relatively conspicuous, birds are mobile and can easily be overlooked (or not heard). Specialized statistical models can be adjusted for imperfect sampling or detection probabilities, yielding more rigorous estimates of occupancy (Royle et al. 2004, MacKenzie et al. 2009). While most analyses have emphasized habitat selection in space, birds also exhibit selection in time, and recent work has offered new analytical approaches that better incorporate temporal aspects of habitat selection (Porzig et al. 2014). However, all approaches for measuring habitat selection are insufficient for examining the fitness consequences of that selection. Thus, ornithologists also work to rigorously measure habitat quality.

Measuring Habitat Quality

There are two basic approaches to conceptualizing how to measure habitat quality. We can either assess habitat quality

directly, by measuring attributes of the habitats themselves, or we can measure variables for individual birds and populations in different habitats to reveal variation in habitat quality. Measuring habitats directly is far less common than measuring indirectly, because measuring directly requires that we know which resources (e.g., specific food items, nest sites) are essential for the species of interest. This is difficult, because we often do not know exactly which resources and ecological conditions are most relevant for many species, and even when we do, they may be difficult (or impossible) to measure. Nonetheless, for some well-studied species, direct measures of habitat quality are possible. For example, Barnes et al. (1995) measured habitat quality for Northern Bobwhite (*Colinus virginianus*) by quantifying grass forage quality, food (insect) abundance, and shrub cover availability. This approach has also been used effectively by Piersma (2012) and his colleagues, who have investigated habitat quality for migratory Red Knots (*Calidris canutus*) by quantifying the availability of prey (mollusks and crustaceans) and competition with other birds. So, while it is possible to use direct measures to measure habitat quality, the far more common approach is to use indirect measures, which we highlight below.

Indirect Measurements—Demography

Most studies take the second conceptual approach and measure avian habitat quality indirectly by quantifying bird abundance, distribution, or performance among different habitats to assess variation in their quality (Johnson 2007). As explained earlier, habitat quality is best defined from an individual bird's perspective as the per capita rate of population increase expected from a given habitat. Thus, the roots of the concept are demographic, and habitat-specific measures of density, reproduction, and survival offer some of the best measures of habitat quality (e.g., Virkkala 1990, Holmes et al. 1996, Franklin et al. 2000, Murphy 2001, Persson 2003). Using the abundance (or density) of birds in habitat is the most common measure of habitat quality, since birds are relatively easy to survey (via point counts or mist nets for example; see chapter 31). Because birds reproduce in discrete nests, reproduction can be ascribed to individual birds and their habitats, rendering nest success, the number of young fledged, and other measures of reproduction common metrics of habitat quality; up to a third of bird habitat studies employ this approach (Johnson 2007). Fewer studies use adult survival as a measure of habitat quality, probably because of the large and lengthy data sets required to assess it rigorously. That said, an increasing number of studies now assess survival, perhaps because of the increased availability and power of survival analysis software (White and Burnham 1999, Murray 2006).

Indirect Measurements—Distribution

Numerous measures of bird distribution can be used to indicate habitat quality based on the theoretical Fretwell-Lucas models suggesting birds should select habitats to maximize their realized habitat quality (box on page 585). Thus, studies that confirm that some habitats are used disproportionate to their availability (ipso facto habitat selection) can reveal high-quality habitat. For example, Hall and Mannan (1999) examined habitat selection to determine what constituted high-quality habitat for Elegant Trogons (*Trogon elegans*) in southeastern Arizona, which highlighted the importance of Arizona sycamore trees (*Platanus wrightii*). Habitat selection models predict that, relative to low-quality habitats, high-quality habitats should be occupied for longer periods within a season and more consistently over years. Consequently, some investigators have used timing, duration, and frequency of habitat occupancy as measures of habitat quality (reviewed by Sergio and Newton 2003). For example, Ferrer and Donázar (1996) found that habitat occupancy was related to both resource availability and reproduction for Imperial Eagles (*Aquila heliaca*) in Spain. Despotism distribution models predict that dominant individuals should settle disproportionately in the highest quality habitats. Therefore, the ratio of behavioral classes among habitats (e.g., adult vs. young, male vs. female) could reveal variation in their quality (Railsback et al. 2003). For example, Rohwer (2004) used age ratios to show that despotic territorial behavior forced yearling male Hermit (*Setophaga occidentalis*) and Townsend's (*Setophaga townsendi*) Warblers into marginal high-elevation habitats for their first potential breeding season, and Marra (2000) found that ratios of dominant to subordinate age and sex classes of wintering American Redstarts varied markedly between high-quality (mangrove) and low-quality (scrub forest) habitats in Jamaica.

Indirect Measurements—Condition

All metrics of habitat quality reviewed in this chapter require measuring populations of birds, which can be problematic for species that are difficult to observe or capture and for birds using habitats only briefly, such as migratory species. As an alternative, some ornithologists have used measures of individual birds' physical condition as indicators of habitat quality. These include external, visible, and measurable features, such as body mass or visible fat deposits, and variables that rely on analysis of sampled tissues (especially blood). For example, Strong and Sherry (2001) found that body mass was a reliable indicator of habitat quality for Ovenbirds (*Seiurus aurocapilla*) wintering in Jamaica, and Seaman et al. (2006) showed that blood plasma metabolites indicated which habitats

afforded the best stopover refueling opportunities for migrating Western Sandpipers in British Columbia and Washington. For further details of the pros and cons of measuring habitat quality with birds' physical condition, see Johnson (2007) and Homyack (2010).

Assumptions

All of these measures of habitat quality carry the assumption that their variation is a consequence of, rather than a cause for, different habitat selection. That is, variation in habitat attributes such as food supply and predation risk must lead to variation in the demographic rates, distribution, or physiological condition of birds. This may often be at least partially true, but can be violated if, for example, strong differences in individual bird quality cause variation in survival or reproduction and also cause birds to use different habitats. For example, Carrete et al. (2006) found that variation in reproduction for eagles (*Aquila chrysaetos* and *A. fasciata*) in southern Spain arose because of changes in bird quality (age) and not because of suitability for breeding per se. Preexisting differences in the condition of birds may also cause them to use different habitats, rendering measures of body condition misleading. For example, lean individuals may choose food-rich but risky habitats, while fat individuals may choose safer but food-poor habitats (Moore and Aborn 2000). In this case, local food supply and body fat would be inversely related, and good body condition would be a poor indicator of food-rich habitats.

More generally, Van Horne (1983) cautioned that the density of animals in a habitat can, in some cases, be a misleading indicator of habitat quality because habitat conditions favoring density, survival, and reproduction may not be the same (Franklin et al. 2000), which could lead to misleading measures of habitat quality if only one parameter is used to rank habitats. Since the publication of her influential and oft-cited paper, biologists recognize that robust measures of habitat quality require a thorough unraveling of habitat-specific measures of demography—i.e., density, reproduction, and survival measures in each habitat considered (Bock and Jones 2004). Time and money constraints rarely allow all of these measures to be obtained, but when multiple measure are obtained, novel insights sometimes emerge. For example, Murphy (2001) learned that annual productivity for Eastern Kingbirds (*Tyrannus tyrannus*) was lower in floodplain than in creek and upland habitats in the Charlotte Valley of central New York, but estimates of survival suggested that all three habitats were population sinks, and numbers were supplemented substantially by emigration from other areas.

Although some empirical evidence indicates that measures of simple abundance can mislead, Bock and Jones (2004) demonstrated that density is usually roughly correlated with

habitat quality for breeding birds. Furthermore, decoupling of density and reproduction was not associated with most environmental and life history attributes as predicted by theory, although their results do suggest that discrepancies emerged most frequently in human-disturbed landscapes. Future work should explore whether density and survival covary over habitats (Johnson et al. 2006).

In this light, the question “which habitat is best?” can be reexamined by asking, how do we measure habitat quality for the relevant management unit (populations), when habitat selection is a process operating at the individual level? To explicate individual habitat quality for population management purposes, we must consider how temporal and spatial scales influence habitat choices and their demographic consequences (Wiens 1989). A habitat's quality can change rapidly for a given species, and care must be taken to understand when resources are most limited and when consequences of habitat occupancy most influence a population (Sherry and Holmes 1995). Sutherland (1998) and Runge and Marra (2005) developed models that articulate the temporal (seasonal) interactions of local habitat quality, availability, and demographics in birds. These models extended previous work describing how individual birds' choices of habitats (based on local quality) impact populations over shorter temporal windows (Orians and Wittenberger 1991, Goss-Custard et al. 1995). These models all demonstrate the delay between birds' habitat choices and their demographic consequences, which should prompt researchers to track birds' fates as long as feasible.

CONSERVATION APPLICATIONS, FROM HABITATS TO LANDSCAPES TO ECOSYSTEMS

Throughout this chapter we have discussed the importance of habitat for bird ecology and conservation. Indeed, the greatest threat to birds, and to biodiversity in general, is habitat loss (Foley et al. 2005; fig. 18.2). In this section, we specify how understanding bird-habitat relationships can advance avian conservation by helping us (1) prioritize habitats for conservation, (2) restore places that have already been degraded, (3) anticipate the response of birds to climate change, (4) incentivize habitat conservation via the provisioning of ecosystem services, and (5) guide key policies to protect habitats for birds. For additional details on bird conservation, see chapters 24–29.

Prioritizing Places and Habitats

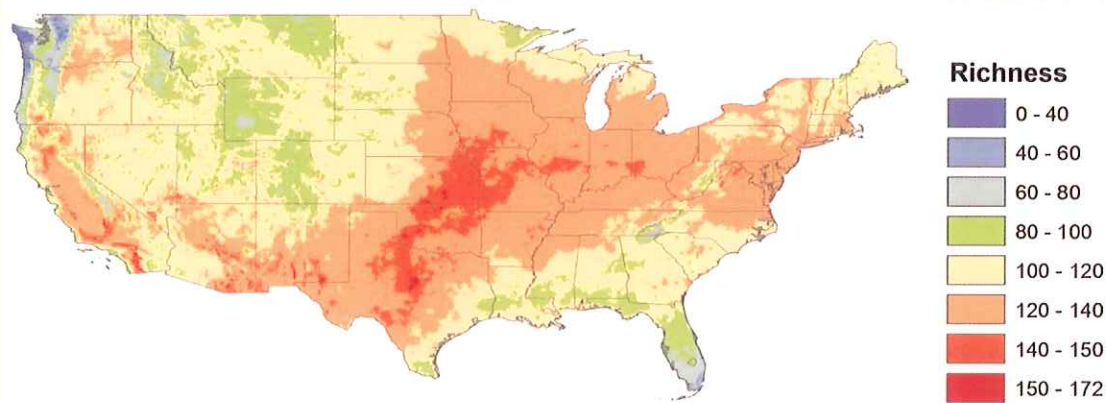
The quantification of bird-habitat relationships has enabled conservation planners to use empirical evidence to prioritize habitats for protection or restoration. Conservation is always limited by time and money, so effective conservation

SPECIES DISTRIBUTION MODELS

By Dr. Brooke Bateman, University of Wisconsin–Madison

Species distribution models (SDMs) are commonly used to characterize and predict species current and future distributions. These models help identify the relationship between where a species occurs and the environmental conditions found at those locations, and to use this information to map a species distribution in geographical space. Maxent (Phillips and Dudík 2004) is a commonly used SDM algorithm that uses presence records of a species and environmental data relating to the locations where that species occurs. Absence data are not needed, as Maxent uses “background” points that are representative of the range of environmental conditions of the study area. The Maxent modeling algorithm discriminates what is unique about the environmental conditions associated with species presence data in comparison to the environmental conditions of the entire study area. With the availability of large datasets that contain bird occurrence data (e.g., e-Bird), we can use modeling techniques such as Maxent to map the potential

distribution of many bird species over large extents. With this information we can map species richness for many species using environmental data such as climate data (see figure). Pairing bird occurrence data with climate data allowed the researchers in this study to explore how climate change in the recent past affected where the potential breeding distributions occurred in the landscape. Given that species distributions are influenced by more than climate alone, these predictions are of a species “potential” distribution or areas where a species could possibly occur based solely on climate conditions. It is also important to note that SDMs use a limited amount of information and that species occurrences are influenced by many factors (e.g., biotic interactions) that may not be included in the model. However, these spatially explicit models of bird distributions can be used to identify priority areas for conservation initiatives and to help understand the potential effects of climate change on species.



Adapted from Bateman et al. 2016. Potential species richness of 285 breeding bird species within the continental United States. Potential species richness is defined as the number of species that have suitable climate within a given grid cell.

action relies on planning that uses ecologically based methods for prioritizing actions (Pressey et al. 2007). Advances in the study of avian habitat selection, especially the increasing availability of empirically based, high-resolution species distribution models (box on page 599), are providing new opportunities to guide on-the-ground decision-making across a wide range of spatial scales (Bayliss et al. 2005, Seavy et al. 2012). For example, ornithologists integrated bird distribution models into conservation activities along the San Joaquin River in the Central Valley of California (Seavy et al.

2012). This work identified synergies in which conservation action for some bird species aligned with other ecological considerations such as flood control and fish habitat. However, they also found that optimal habitat conditions varied among groups of birds, demanding planners to balance trade-offs in predicted effects on target species. They concluded that one-on-one interactions between the ornithologists that develop the models and the decision-makers that use them are essential to best inform conservation and restoration (Seavy and Howell 2010). This work is clearly vital

for bird conservation, but birds are often used as indicators of environmental condition in general (Hilty and Merenlender 2000), so bird-habitat relationships can typically be used to inform priorities for broader conservation agendas. For example, areas with a large proportion of unique bird species—Endemic Bird Areas—have been used to identify sites of global conservation priority (Wilson et al. 2006).

Ecological Restoration

Where habitat has already been degraded, conservationists can use understanding of bird-habitat relationships to optimize habitat restoration. For example, Kus (1998) used species-specific models of habitat suitability for endangered Least Bell's Vireo (*Vireo bellii pusillus*) to confirm that restored sites were developing vegetation characteristics of intact natural habitat, and found that occupation of restored sites for breeding took several years, but was accelerated by the presence of adjacent mature riparian habitat. Gardali and Holmes (2001) found that riparian bird species responded favorably to particular local restoration practices such as the number of tree species planted and the planting tree density of certain species. However, they also found that birds responded to the amount of riparian forest in the surrounding landscape, again highlighting the importance of landscape-level conservation planning in habitat restoration.

Climate Change

In addition to habitat loss, climate change poses a major threat to bird conservation (fig. 18.2), and understanding bird-habitat relationships is vital for predicting how birds respond to climate change. For example, in New York, Zuckerberg et al. (2009) found that the population center for 129 bird species has shifted northward by over 4 km over the past 30 years, which provided strong evidence that birds are indeed shifting their ranges poleward in response to climate change. Further, as species shift in response to climate change, novel communities (i.e., those with no natural analog) are being formed (Stralberg et al. 2009a, Prince and Zuckerberg 2015). In the eastern portions of North America, the wintering distribution of 38 bird species responded strongly, with more southerly species shifting their ranges northward in response to milder winter temperatures (Prince and Zuckerberg 2015). While we now understand that species assemblages are responding strongly to climate change (Prince and Zuckerberg 2015), it remains unclear how climate change will affect avian biodiversity in the long run (Walther et al. 2002). Bird-habitat relationships are helping conservationists plan for climate change by enabling forecasts of bird distributions aimed at either protecting

habitats likely to be needed in the future (e.g., Benitez-Lopez et al. 2014) or identifying climate refugia from anticipated climate change (e.g., Stralberg et al. 2015). While much work has focused on montane birds' responses to rising temperature (Elsen and Tingley 2015), modeling effects of estuarine habitat in the face of sea level rise is vital for coastal birds (Veloz et al. 2013). Other approaches have used species-habitat models to prioritize habitats that will maintain connectivity, which may be necessary for species to shift their distribution as the climate warms (Mazaris et al. 2013, Jones et al. 2016).

While global climate change is prompting gradual shifts in temperature and precipitation, more immediate and potentially more detrimental consequences to birds come from extreme weather events such as prolonged droughts, cold snaps, tornado outbreaks, or severe storms, which have greatly increased in frequency and intensity over the past few decades (Cai et al. 2014, Conrey et al. 2016), often with negative consequences on biodiversity (Parmesan et al. 2000, McCreedy and van Riper III 2014). For birds, extreme weather can lead to changes in distribution (Albright et al. 2009), disrupt avian community structure (Rittenhouse et al. 2010), alter migratory pathways (Streby et al. 2015), and lead to mass mortality events (McKechnie and Wolf 2009). Additionally, extreme weather can alter phenological relationships of migratory birds and their seasonal resources. There is strong evidence that migratory birds time their spring migrations to match the peak availability of caterpillars and other protein-rich prey (Graber and Graber 1983), and any disruptions in the delicate timing of these events could be detrimental for birds (Kellermann and van Riper 2015). For example, throughout Europe, there is evidence that migratory birds that do not arrive to their temperate breeding locations in coincidence with peaks in food availability have lower breeding success (Møller et al. 2008). Many insects in North America emerge coinciding with plant budburst, but Neotropical-Nearctic migrant birds are unable to adjust their migratory timing to match the early phenology of the insect food resources (Wood and Pidgeon 2015). Without the migratory birds present to consume herbivorous insects, vegetation damage is high, which highlights a potential negative consequence caused by extreme weather (Wood and Pidgeon 2015). In theory, understanding bird-habitat relationships could help conservationists seeking ways to mitigate effects of extreme weather, which remains an urgent research need. For highly mobile species like birds, movement away from extreme climatic events may be a viable response, even for species that normally show high site fidelity (Martin et al. 2007). Applying our understanding of bird-habitat relationships could help us prioritize refugia from weather extremes,

which could occur, for example, at the edges of species' ranges or at key geographic locations along migratory pathways (Bateman et al. 2015).

Dynamic Conservation

While understanding avian habitat ecology can certainly help us respond to future conservation needs of birds, it can also be used to guide current, real-time conservation. For example, an innovative collaboration between The Nature Conservancy, Cornell Lab of Ornithology, and Point Blue Conservation Science uses data on bird distribution to predict where wetland management can best benefit shorebirds and waterfowl during their migrations. By crunching data from eBird, ecologists can overlay maps of bird distribution with aerial views of existing surface water, revealing where the birds' need for habitat is greatest (Robbins 2014). Funding from The Nature Conservancy then pays rice farmers in the birds' flight path to keep their fields flooded with irrigation water to provide habitat for migrating flocks. This work also underscores the power of economic incentives for the conservation of bird habitat, a topic that has received much recent attention by ornithologists and economists examining so-called ecosystem services (Whelan et al. 2008, Wenny et al. 2011).

Ecosystem Services

Conserving birds demands that we protect their habitats, so it is imperative that policies incentivize habitat conservation. Strong environmental policies can protect habitat on public lands and for species protected by government regulations, such the US Endangered Species Act, but incentives that apply for common birds and on private lands are also needed (Kareiva and Marvier 2007, Armsworth et al. 2012). Recent conservation research has emphasized that valuing ecosystem services can provide these incentives (Gómez-Baggethun et al. 2010). Ecosystem services are process that help sustain and fulfill human life (Daily 1997). Examples of ecosystem services provided by birds include pest control (a regulation service, Johnson et al. 2010), and seed dispersal (a supporting service, Hougner et al. 2006), and recreational and aesthetic value (a cultural service, Gürlük and Rehber 2008). By explicitly linking the provisioning of these services to bird habitat, an incentive for habitat conservation can materialize. For example, Kellermann et al. (2008) and Railsback and Johnson (2014) found that warblers in Jamaica help control economically damaging insect pests in coffee farms, and that the delivery of this pest control service was enhanced by the conservation of trees and forest patches both within and beyond the farms' boundaries. Cultural values, such as aesthetic appreciation, may be more difficult to quantify than

other ecosystem services, but they can also provide incentives for habitat conservation. Neumann et al. (2009) conducted an analysis of real estate prices near the Great Meadows National Wildlife Refuge in Massachusetts, a popular place for bird-watching. They found that properties located close to the refuge had a demonstrable price premium, providing incentive for landowners and city planners to ensure the protection of habitats for birds and other wildlife.

Habitat and Policy

Many governments have recognized the central role of habitat protection in the conservation of biodiversity, passing legislation that provides protection of habitat considered "critical" (Camaclang et al. 2015). These laws, such as the US Endangered Species Act (ESA 1973), Australia's Environment Protection and Biodiversity Conservation Act (EPBC 1999), and Canada's Species at Risk Act (SARA 2002), necessarily combine with science to specify how these critical or essential habitats should be defined and designated for a given species. This law-science relationship and its effect on habitat policy was exemplified in a 1994 Supreme Court case concerning the Northern Spotted Owls mentioned at the start of this chapter, a case now regarded as one of the most important in American conservation history (Petersen 2002, Alagona 2013). The ESA makes it illegal to "harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, collect or attempt to engage in any such conduct" toward a listed species, actions collectively called a "take" in the lexicon of ESA. In the 1994 case of *Babbitt v. Sweet Home Chapter of the Communities for a Great Oregon*, the Supreme Court ruled in a six to three majority that science indicates the word "harm" in this case must include habitat modification. This ruling firmly linked the legal protection of species with the protection of their habitats, and the ESA has since become a model for analogous legislation around the world (Camaclang et al. 2015). The concepts of endangered species and habitat, thus affected by this law-science relationship, are no longer possible to examine without referring to both science and the law (Ruhl 2007, Alagona 2013).

To advance the conservation of birds, our efforts must prioritize habitat conservation. Our view is that recognizing the reliance of birds on their habitats, incentivizing avian conservation by valuing ecosystem services, and aiming environmental policy toward the protection of species and their habitats are powerful tools for conservation and for improving human life. But these tools should be used alongside recognition of the intrinsic value of birds (Gavin et al. 2015), because regardless of how birds may benefit human livelihood and fulfillment, they are also simply our co-inhabitants on this planet.

KEY POINTS

- Habitat is an area with the resources and conditions that promote occupancy by individuals of a given species and allows those individuals to survive and reproduce.
- To balance species conservation and human needs, we must understand the nuances of **habitat selection**—the study of where birds live and why.
- Habitat quality is best considered from individual birds' perspectives as the per capita contribution to population growth expected from a given habitat. This is best measured as directly as possible; indirect measures are far more efficient, but their accuracy must be verified.
- The availability and quality of habitats often limit or regulate bird populations.
- Advances in remote measurements have significantly propelled the study of bird habitats, but they have also led researchers to focus on incomplete assessments of habitat, such as an overreliance on vegetation. Recent work is rightly focusing on the resources and conditions underlying spatial variation in the performance of birds.
- Habitat ecology strongly affects environmental policies, which carry enormous social and economic consequences.
- Other factors can interact with or in some cases overwhelm habitat in driving bird populations, and ornithologists must be aware of the range of processes affecting wild birds.

KEY MANAGEMENT AND CONSERVATION IMPLICATIONS

- Practitioners must understand the role of habitat in limiting and regulating bird populations.
- It is vital to recognize spatial and temporal variation in habitat quality to prioritize habitats for conservation effectively.
- Ornithologists should examine how global and landscape-scale dynamics can affect local habitat selection and quality in order to optimize habitat management, restoration, and acquisition.
- Traditional habitat conservation—identifying habitats to preserve, restore, and manage—remains an important tool for bird conservationists. But newer, innovative approaches are opening additional opportunities to integrate the needs of birds and people.
- The instrumental value of services that birds provide can be harnessed to incentivize conservation, while acknowledging the intrinsic value of birds.

DISCUSSION QUESTIONS

1. What is the difference between vegetation type and habitat, and why is the latter a better concept for understanding the distribution of birds?
2. How can the quality and quantity of habitat regulate a bird population—that is, cause it to rise when it is below a long-term average and decrease when it is above a long-term average?
3. Can you think of a scenario in which there is a discrepancy between habitat quality from the perspective of an individual bird and from a population perspective?
4. If conservationists are trying to identify the highest quality habitats for conserving a threatened bird species, why does it matter whether the species more closely follows an ideal free or an ideal despotic distribution?
5. How can the presence of conspecifics favor the selection of habitat by birds? How can the presence of conspecifics disfavor the selection of habitat by birds? What natural history attributes might make one of these outcomes more likely than the other for a species?
6. Birds are rarely 100 percent detectable. How does that reality affect the design of studies of avian habitat selection? Specifically, how does imperfect detection affect “used vs. unused” and “unused vs. available” study designs?
7. How can species distribution models prioritize habitats for avian conservation in the face of climate change?
8. What is the legal link between habitat and the Endangered Species Act?

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