

MEASURING HABITAT QUALITY: A REVIEW

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Abstract. Understanding habitat quality for birds is crucial for ecologists and managers, but few papers have explored the advantages and disadvantages of different ways to measure it. In this review I clarify terminology and distinguish habitat quality from related terms, differentiate habitat quality at the levels of individual birds and populations, and describe different field methods for measuring habitat quality. As much as feasible, biologists concerned with habitat quality should emphasize demographic variables while recognizing that reproduction, survival, and abundance may not all be positively correlated. The distribution of birds can also reveal habitat quality (e.g., through patterns of habitat selection), but researchers should first investigate how closely their subjects follow ideal distributions because numerous ecological factors can lead birds to select poor and avoid rich habitats. Measures of body condition can provide convenient measures of habitat quality, but to be useful they must be a consequence, rather than a cause, of habitat selection. Habitat ecologists should use caution before relying on shortcuts from more labor-intensive demographic work. To increase the reliability of our habitat quality measurements, we should work to develop new methods to assess critical assumptions of nondemographic indicators, such as whether birds follow ideal distributions under natural conditions and whether spatial variation in body condition manifests in differential fitness.

Key words: *body condition, demography, distribution, habitat preference, habitat quality, habitat selection, habitat suitability.*

Mediciones de Calidad de Hábitat: Una Revisión

Resumen. Entender la calidad del hábitat de las aves es crucial para los ecólogos y los encargados del manejo ambiental, pero pocos artículos han explorado las ventajas y desventajas de distintos métodos para medirla. En esta revisión, aclaro la terminología y diferencio la calidad del hábitat de otros términos relacionados, distingo la calidad del hábitat a nivel de aves individuales y de poblaciones y describo diferentes métodos de campo para medir la calidad del hábitat. En la medida de lo posible, los biólogos interesados en la calidad del hábitat deberían enfatizar variables demográficas, y tener en cuenta que la reproducción, supervivencia y abundancia podrían no estar correlacionadas. La distribución de las aves también puede indicar la calidad del hábitat (e.g., a través de patrones de selección de hábitat), pero los investigadores deberían primero investigar hasta qué punto sus sujetos de estudio presentan distribuciones ideales, debido a que muchos factores ecológicos pueden llevar a que las aves seleccionen ambientes pobres y eviten ambientes ricos. Las medidas de condición corporal también pueden representar medidas convenientes de la calidad del hábitat, pero para ser útiles deben ser una consecuencia y no una causa de la selección de hábitat. Los ecólogos ambientales deben tener cuidado al basarse en estudios rápidos en lugar de realizar trabajos demográficos más laboriosos. Para incrementar la confiabilidad de nuestras medidas de calidad de hábitat, debemos desarrollar nuevos métodos para abordar las suposiciones más importantes de los indicadores no demográficos, tales como si las aves presentan distribuciones ideales en condiciones naturales, y si la variación espacial en la condición corporal se traduce en una adecuación biológica diferencial.

INTRODUCTION

Local habitat affects the fitness of animals through variation in resources and environmental conditions (Bernstein et al. 1991, Pulliam 2000). Spatial and temporal variation in

habitat conditions thus generate strong selective pressure for habitat selection (Cody 1985), which in turn influences reproduction and survival of individual birds (Brown 1969, Fretwell and Lucas 1970, Sutherland and Parker 1985), and contributes to the regulation of bird populations (Newton 1998). It is no surprise, then, that ornithologists have long recognized the need to understand variation in habitat for birds (Block and Brennan 1993).

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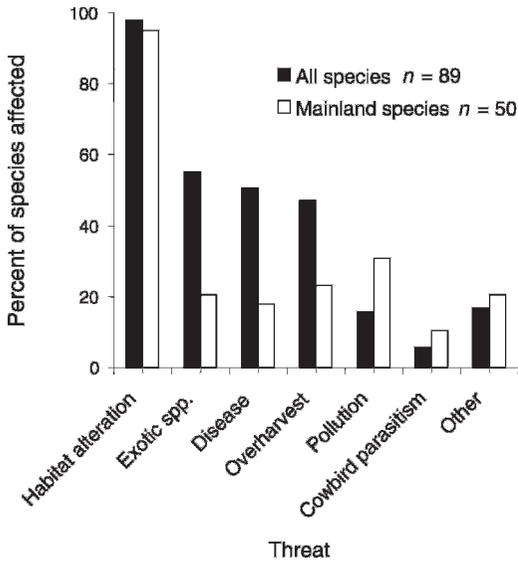


FIGURE 1. Causes of endangerment of bird species listed as threatened and endangered in lands managed by the United States. “All species” includes data from Hawaii, Puerto Rico, American Samoa, and other islands; “mainland species” excludes those from islands. A species can have more than one cause of endangerment. Note that habitat alteration—which includes habitat loss, degradation, and conversion—is by far the greatest threat, followed by interactions with exotic species, which often invade following habitat alteration. The data in this figure were obtained from the Federal Register and cover all species listed as of 5 April 2006.

Indeed, loss and degradation of habitat is the greatest threat to wild bird species (Fig. 1). Limited funding requires prioritizing habitats based on their value for particular research questions or management objectives, which often revolve around focal species such as those of special conservation concern. How can habitats be judged for their importance to birds; how can good, marginal, and poor habitats be distinguished? That is, how can we assess the *quality* of habitats?

Van Horne (1983) provided a foundational treatment of habitat quality for vertebrates and cautioned that the density of animals in a habitat can, in some cases, be a misleading indicator of habitat quality. Since the publication of her influential and oft-cited paper (Bock and Jones 2004), biologists have recognized 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). However, time and monetary constraints rarely allow all of these measures to be obtained, so biologists often rely on other measures to help distinguish rich and poor habitats, spawning related terms and concepts such as habitat carrying capacity, habitat preference, habitat occupancy, and so on. In many cases, habitat quality is regarded as a somewhat vague concept enabling habitat patches to be ranked, and it is often simplified into an index ranging from 0 to 1, as in the U.S. Fish and Wildlife Service’s “habitat suitability index” (HSI) models (Schamberger et al. 1982). Despite its importance to the discipline and the myriad recognized ways it can be measured, there have been few reviews of habitat quality and how it can be quantified by ornithologists (but see introductions of James 1971, Bernstein et al. 1991, Block and Brennan 1993, Sergio and Newton 2003, Pidgeon et al. 2006). Here, I describe ways of conceptualizing and measuring habitat quality. Specifically, I have four objectives: (1) clarify terminology and distinguish habitat quality from related terms, (2) differentiate habitat quality at individual and population levels, (3) outline various ways of measuring habitat quality for wild birds, recognizing methods that emphasize demographic, distributional, and individual condition variables, and (4) review how ornithologists have measured habitat quality in the last two decades.

BACKGROUND AND TERMINOLOGY

Hall and her colleagues (Hall et al. 1997, Morrison and Hall 2002) argued that some of the confusion surrounding habitat’s role in animal ecology stems from inconsistent and imprecise use of terms, which is unsurprising given habitat’s long history in ecology (Grinnell 1917, MacArthur et al. 1962, James 1971, Whittaker et al. 1973). Hall et al. (1997:175) sought to provide standards, and they defined habitat as “the resources and conditions present in an area that produce occupancy—including survival and reproduction—by a given organism.” This is the definition of habitat used in this paper. Hall et al. (1997) considered habitat quality as the ability of the environment to provide conditions appropriate for individual and population persistence. This is an intuitive and attractive operational definition of habitat quality, but much is masked by considering habitat quality to relate to both individual- and

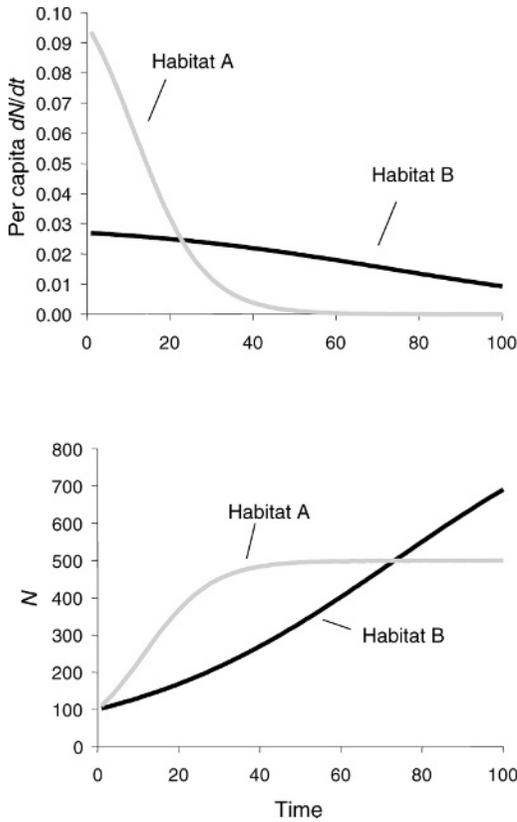


FIGURE 2. Logistic population growth curves for birds in two hypothetical habitats. Habitat A has relatively few high-quality resources and Habitat B has abundant lower-quality resources, resulting in a higher intrinsic rate of population growth in A ($r_A = 0.12$, $r_B = 0.03$) and a higher carrying capacity in B ($K_A = 500$, $K_B = 1000$). Both populations were simulated with initial population sizes of 100 and run for 100 time intervals. If habitat quality is considered purely from an individual bird's perspective, then Habitat A is the better habitat until time 23, after which point Habitat B offers the higher average per capita dN/dt . In contrast, if habitat quality is measured as the current population size, then Habitat A remains better until time 74. If habitat quality is considered the maximum sustained population size, as may be the perspective of many conservationists, then Habitat B is always better because it has the higher carrying capacity.

population-level perspectives. For example, consider two habitats: Habitat A has relatively few high-quality resources and Habitat B has abundant lower-quality resources (Fig. 2). The details of the resources are unimportant; they could be nest sites for a songbird or rodent prey for a raptor, for example. Habitat A offers the

higher intrinsic rate of population growth (r) and Habitat B has a higher carrying capacity (K). Which habitat is better? From an individual bird's perspective, Habitat A is better in many respects because it offers access to high quality resources that maximize a bird's chances for survival and reproduction. However, at a population level, Habitat B may be better because it supports a larger persistent local population. This trade-off in quality and quantity of resources was explored by Hobbs and Hanley (1990), and it underscores the necessity of distinguishing habitat quality from the perspective of individual animals, which seek to maximize their own fitness, from the perspective of conservationists concerned with populations (Pidgeon et al. 2006).

Organisms 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 (Newton 1989, Block and Brennan 1993, Franklin et al. 2000). Natural selection therefore favors the capacity for individuals to distinguish high and low quality habitats (Clark and Shutler 1999). 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 (1989b) considered this contribution to an organism's fitness the *habitat fitness potential*, which provides the theoretical basis for habitat quality (Garshelis 2000, Railsback et al. 2003). For example, Franklin et al. (2000) quantified habitat fitness potential for Northern Spotted Owls (*Strix occidentalis caurina*) as the relative contribution to the overall population of individuals occupying a given habitat. 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 time (Coulson et al. 2006) and provides the definition of habitat quality used throughout this paper.

Over most population densities, intraspecific competition diminishes the fitness conferred upon a habitat's occupants (Rodenhouse et al. 2003, Sillett et al. 2004). Note, however, that low population densities can suppress fitness if

mate selection is constrained (see review of Allee effects by Stephens and Sutherland [1999]), and high density can be attractive to an individual if conspecifics are useful cues for resources insensitive to density-dependent competition (see reviews by Stamps 1991, Ahlering and Faaborg 2006) or for species that enjoy marked benefits of sociality. Thus, theoreticians distinguish the quality of habitat in the absence of competition, called *fundamental habitat quality*, from the quality actually experienced by competing occupants, called *realized habitat quality*. Under an ideal free distribution (Fretwell and Lucas 1970), equal competitors select habitats to maximize their individual fitness. At equilibrium, individuals are distributed among habitats that vary in fundamental habitat quality (also called intrinsic or inherent habitat quality or zero-density suitability sensu Bernstein et al. [1991]) such that all individuals experience the same realized habitat quality (Fig. 3). Under ideal despotic distributions or mixed models, individuals are unequal competitors and preemption of resources or territories in the highest quality habitats ensures that the strongest competitors reap the greatest rewards (Parker and Sutherland 1986). Thus, at equilibrium the average fitness conferred by a habitat on its occupants—realized habitat quality—is lower in habitats with low fundamental habitat quality (Fig. 3).

The distinction between these models is important because they can yield opposing prioritization 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 higher in quality and should be prioritized for conservation. 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 strong competitors, the density of birds in poor habitats is likely to be higher than that in rich habitats (Bernstein et al. 1991). In this case, density will be a misleading indicator of habitat quality, and prioritizing habitats should involve measuring the performance of individual birds to assess variation in realized habitat quality.

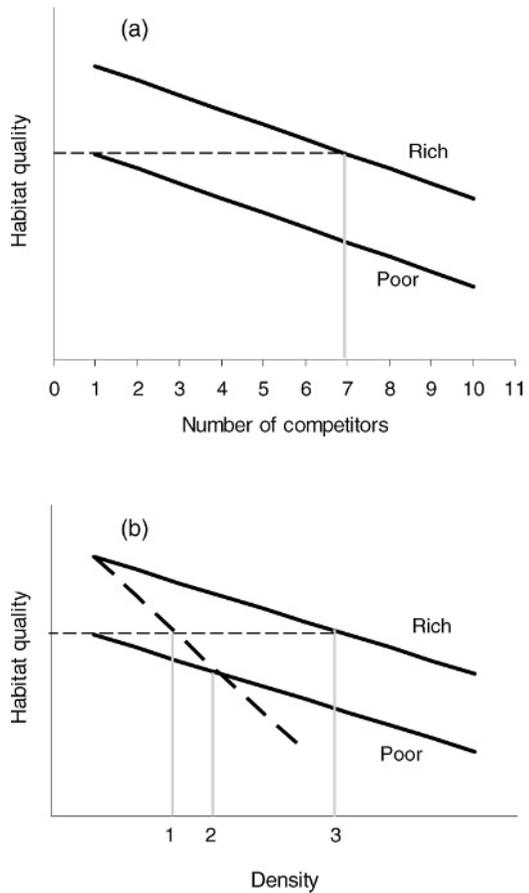


FIGURE 3. Models of (a) ideal free and (b) ideal despotic distributions (from Fretwell and Lucas 1970, Parker and Sutherland 1986, Bernstein et al. 1991). Two habitats varying in quality are modeled; each shows a linear density-dependent decline in quality. Fundamental habitat quality is the intrinsic 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 seven and one, respectively (depicted by horizontal dashed line). In the despotic distribution model, competitors are unequal. As density increases, weak competitors (diagonal 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.

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 understand individual habitat quality for population management purposes, we must consider how temporal and spatial scales influence habitat choices and their demographic consequences (Wiens 1989a, Lambrechts et al. 2004). 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 to articulate the temporal (seasonal) interactions of local habitat quality, availability, and global 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, Caldow et al. 1995). These models all evince the delay between birds’ habitat choices and their demographic consequences, which should prompt researchers to track their birds’ fates as long as possible.

Spatially, a bird’s use of the landscape can vary dramatically, with some areas (even within its home range) nearly ignored while other receive intense use (Manley et al. 2002). Thus, fine scales of habitat selection (e.g., Johnson’s [1980] 2nd and 3rd orders) must be understood to fully uncover nuanced spatial patterns of habitat quality. Moreover, some birds may not achieve adequate fitness unless multiple habitats are juxtaposed in ways that enable them to meet all their life history requirements (Gullion 1984, 1988). Consequently, population viability may be strongly influenced by the composition of rich and poor habitat patches in a landscape (Pulliam 1988, Dunning et al. 1992, Wiens 2000), underscoring the importance of examining habitat quality over large spatial extents (Pulliam 1988, Howell et al. 2000, Fahrig 2003). Thus, ecologists should focus on the individual consequences of habitat occupancy across a landscape (i.e., indicators of habitat quality) to inform land management decisions, because these consequences ultimately manifest in population dynamics (Sutherland 1996). Indeed,

measuring habitat quality for individual wild animals is a necessary precursor for discerning effects of landscape composition on population dynamics (Pulliam 2000, Runge et al. 2006).

MEASURING HABITAT QUALITY

SURVEY OF THE LITERATURE

To assess how ornithologists have measured habitat quality, I reviewed papers published in the last 21 years (1984 to 2005). I chose 1984 as a start date because it was the first full publication year following the publication of van Horne’s (1983) *Density as a misleading indicator of habitat quality*; 2005 was the latest year with complete database records at writing. I searched titles, abstracts, and key words for the term habitat (or patch) adjacent to the term quality (or suitability). Searches in nonornithological journals also included the term bird. I limited my search to 27 journals, chosen based on their relevance to avian habitat ecology (listed in decreasing number of retrieved titles): Auk, Journal of Avian Biology (Ornis Scandinavica), Journal of Wildlife Management, Condor, Journal of Animal Ecology, Journal of Applied Ecology, Ibis, Conservation Biology, Ecology, Journal of Field Ornithology, Waterbirds, Oikos, Proceedings of the Royal Society of London Series B, Wilson Bulletin, Oecologia, Journal of Raptor Research, American Midland Naturalist, Behavioral Ecology, American Naturalist, Science, Behavioral Ecology and Sociobiology, Nature, Trends in Ecology & Evolution, Conservation Ecology, Animal Conservation, Animal Biodiversity and Conservation, and Proceedings of the National Academy of Sciences USA. I surveyed papers using the Wildlife and Ecology Studies Worldwide database (<http://biblioline.nisc.com/scripts/login.dll>), which has a complete index of surveyed journals since 1984 (or since first publication for newer journals). Papers were first examined to determine whether authors either claimed to have measured habitat quality empirically or drew conclusions concerning habitat quality based on the data presented. For each paper satisfying this requirement, I classified how habitat quality was measured, tallying one or more of the 12 categories of measurements listed in Table 1 and described in more detail in the following section. I summarized results by calculating the percentage of

TABLE 1. Percentage of 173 ornithological studies published in 27 journals between 1984 and 2005 that used various measures of habitat quality. Twelve different types of measurements were grouped into two basic approaches, one of which was subdivided into three general categories (demographic, distributional, and individual condition measurements). Percentages often combine to more than 100% because many studies used more than one habitat quality measurement.

Measurements of habitat quality	% of studies
Measure habitat attributes directly	37
Resources	23
Environmental constraints	6
Crude correlates	15
Measure birds to reveal habitat quality	74
Demographic measures	53
Density or abundance	26
Reproduction	37
Survival	10
Distributional measures	31
Habitat selection (spatial patterns)	19
Occupancy (temporal patterns)	7
Arrival or departure patterns	2
Behavioral or age class distribution	6
Individual condition measures	9
Morphological variables	7
Physiological variables	3

total papers that used each category of habitat quality measurement. Many studies measured habitat quality in multiple ways, with an average of 1.6 ± 0.1 SE types of measurements used in each study (range: 1–6). Of 241 papers identified by the database search, 173 measured habitat quality empirically and were included in this review.

BASIC APPROACHES

There are two basic approaches to conceptualizing how to measure habitat quality. We can either assess habitat quality directly by measuring attributes of a habitat itself, or we can measure variables for individual birds and populations in different habitats to reveal variation in habitat quality. In measuring habitats directly, we should of course be concerned with critical resources, such as food and nest sites. Yet habitat is far more than the vegetation and resources surrounding an animal. Equally important are the ecological constraints that may limit the use of those resources, such as risk of predation, intensity of competition, and physical accessibility of resources. Indeed, habitat is defined not only by

the resources necessary for survival and reproduction, but also by the conditions that constrain their use (Morrison et al. 2006).

Relatively few studies measuring habitat attributes directly do so in an attempt to explicitly measure habitat quality. That is not to say few studies measure vegetation and resources as a means to describe habitat. To the contrary, the literature is rife with studies relating animal distribution or demography to aspects of habitat, especially vegetation (Scott et al. 2002, Morrison et al. 2006). Yet, few of these studies consider vegetation metrics to be measurements of habitat quality. Instead, they rank the quality of habitats based on the abundance, distribution, or performance of birds inhabiting them and use statistical associations with habitat measurements to identify features potentially contributing to a habitat's quality. This descriptive approach to examining wildlife-habitat relationships is of limited use (Morrison 2001), and experimental work is underutilized to test hypotheses relating habitat quality to features of the landscape humans can potentially influence, such as vegetation cover, forest stand characteristics, habitat fragmentation, and so on.

Nonetheless, the features hypothesized to govern habitat quality are feasibly quantified in some systems, allowing habitat quality to be measured directly. For example, Barnes et al. (1995) measured habitat quality for Northern Bobwhites (*Colinus virginianus*) by quantifying grass forage quality, food (insect) abundance, and availability of cover. Rodenhouse et al. (2003) evaluated habitat quality for nesting Black-throated Blue Warblers (*Dendroica caerulescens*) by surveying for nest predators, quantifying shrub density, and calculating caterpillar and spider biomass in individual birds' territories. Goss-Custard, Clarke et al. (1995) documented food availability and competition to quantify habitat quality for Oystercatchers (*Haematopus ostralegus*). These approaches assume we understand (or can work to learn) which resources and environmental conditions actually influence habitat quality for birds, and they require we devise techniques to measure these attributes accurately. In well-studied species like those cited above, researchers have worked toward this goal. However, we simply do not know enough about many bird species to follow this approach. Among the 173

papers reviewed, less than 25% quantified resources available to birds, and only 6% quantified how predation, competition, or other factors affected a habitat's quality (Table 1). Without adequate knowledge of critical resources and constraints and established protocols for how to measure them, researchers aiming to assess avian habitat quality directly may be tempted to use crude vegetation measurements (often gross vegetation type) as surrogates for habitat quality, which is unlikely to yield worthwhile results. Nonetheless, about 15% of the studies reviewed followed this approach. For many systems, it will be more efficient and meaningful to evaluate habitat quality by studying birds in different habitats, using variation in their demographics or performance to reveal variation in habitat quality.

MEASURING BIRDS TO REVEAL HABITAT QUALITY

Most studies take the second conceptual approach by quantifying bird abundance, distribution, or performance among different habitats to assess variation in habitat quality (Table 1). Few studies can measure all of these potential indicators of habitat quality simultaneously, and it is not always clear which measure is most appropriate. Here, I classify these bird-based indicators of habitat quality into three broad groups—demographic, distributional, and individual condition measures—and describe some strengths and limitations of each.

Some authors have also used behavioral observations as proxies for other measures of habitat quality. For example, Lyons (2005) used foraging behaviors as measures of food supply to deduce habitat quality for Prothonotary Warblers (*Protonotaria citrea*), Vickery et al. (1992) introduced the idea of measuring adult behavior to reveal likely nesting outcomes without the need to locate nests, and Brown and his colleagues (Brown 1988, Kohlmann and Risenhoover 1996) pioneered the use of the residual density of food in artificial food patches (“giving up density”) to reveal costs associated with foraging, such as predation risk. These measures can certainly advance our understanding of avian habitat ecology, but because they usually reveal only a portion of a habitat's value (foraging value and in some

cases also predation risk), they are not included in this review.

Demographic measures. 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 (Virkkala 1990, Holmes et al. 1996, Franklin et al. 2000, Murphy 2001, Persson 2003, Knutson et al. 2006). Using demographics to measure habitat quality assumes the parameters are both measurable and attributable to habitat. Over half of the papers reviewed used at least one form of demographic parameter to assess habitat quality (Table 1). Most studies involving demographic measures of habitat quality focused on abundance or reproduction, perhaps reflecting a bias toward temperate-breeding bird species. Only 10% of the studies measured adult survival, probably because of the large and lengthy datasets required to assess it rigorously. However, survival assessments have recently become more frequent, perhaps due to the increased availability and power of survival analysis software (White and Burnham 1999, Murray and Patterson 2006). Over 23% of the studies employing demographic measures of habitat quality published in 2001 or later included measures of survival, whereas only 8% did so prior to 2001 ($\chi^2_1 = 3.9$, $P = 0.05$).

The chief disadvantage of demographic measures of habitat quality is that they are difficult to obtain. Only 4% of the papers reviewed included simultaneous estimates of density, reproduction, and survival (for classification purposes, I considered assessments of nest survival as measures of reproduction). In each of these exemplary cases, however, a broad understanding of habitat quality was obtained. For example, Holmes et al. (1996) discovered that high shrub density was associated with high bird density, high per capita fledging success, and low mortality (or emigration) for Black-throated Blue Warblers in New Hampshire; Franklin et al. (2000) confirmed that the highest reproductive and survival rates for Northern Spotted Owls in northwestern California were in areas containing mosaics of old and young forests, whereas too much of one forest age or the other was associated with

diminished fitness potential; and Murphy (2001) learned that annual productivity of 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 whose numbers were supplemented substantially by immigration.

Quantifying multiple indicators of habitat quality is, in theory, critically important, 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. Van Horne (1983) and Vickery, Wells et al. (1992) provided hypothetical scenarios and empirical examples in which density was high while reproduction was low. However, Bock and Jones (2004) demonstrated that density was usually roughly correlated with habitat quality for breeding birds, and that decoupling of density and reproduction was not associated with most environmental and life history attributes predicted by theory, although discrepancies emerged most frequently in human-disturbed landscapes. Future work should explore whether density and survival covary over habitats (Johnson et al. 2006). Ecologists should also continue to explore new field techniques to feasibly measure previously elusive demographic parameters. For example, tracking the survival of small migratory birds from space may be possible with the international space station (Cochran and Wikelski 2005), biomarkers may make possible the estimation of population size (Garshelis and Visser 1997) and reproduction (Hebert and Wassenaar 2005) over large areas, and stable isotopes can link habitat-specific demographics with habitat choices made by birds in previous seasons (Marra et al. 1998, Gunnarsson et al. 2005).

Distributional measures. The ideal free and ideal despotic distribution models provide the theoretical backdrop for how animal distribution may reveal variation in habitat quality (Fig. 3). The measures all share the assumptions that: (a) birds have (or can quickly obtain) perfect knowledge of realized habitat quality, (b) birds select habitats that maximize their individual fitness, (c) there are no dispersal or

selection costs, and (d) there are no “time lags” (birds remaining distributed according to previous rather than current habitat quality; Wiens 1989b).

Numerous measures of bird distribution can be used to indicate habitat quality based on these models. The disproportionate use of a habitat relative to its availability—called habitat selection (Jones 2001)—can indicate high-quality habitats, and the field and analytical methods to investigate habitat selection are well described (Manly et al. 2002, Morrison et al. 2006, Thomas and Taylor 2006). Of the papers reviewed, 19% employed habitat selection as a measure of habitat quality. For example, Hunt (1996) used patterns of habitat selection to evaluate habitat quality for American Redstarts (*Setophaga ruticilla*) breeding along a successional gradient in New England; 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 sycamore trees (*Platanus wrightii*); and Hirzel et al. (2004) used habitat selection to assess habitat quality for the first Bearded Vultures (*Gypaetus barbatus*) reintroduced into the European Alps to inform future releases.

The principal weakness in using distribution to reveal habitat quality is that numerous scenarios can lead to animals selecting poor and avoiding rich habitats (Rapport 1991, Railsback et al. 2003), including incomplete information (Shochat et al. 2002, Stamps et al. 2005), ecological traps (Battin 2004), time lags and site fidelity (Davis and Stamps 2004), strong despotic distributions (Parker and Sutherland 1986), a lack of high-quality habitat (Halpern et al. 2005), and others (Bernstein et al. 1991, Block and Brennan 1993, Kristan 2003). Thus, researchers should first establish how well a given system adheres to patterns of ideal habitat selection before using animal distribution to reveal variation in habitat quality (Clark and Shutler 1999, Pulliam 2000, Morris 2003, Zimmerman et al. 2003). This is, of course, easier said than done, since the very incentive for interpreting bird distribution as a measure of habitat quality is because measuring fitness itself is often impractical. Nonetheless, density-dependent habitat selection models (e.g., ideal free and ideal despotic

models) can be examined with techniques that do not require quantifying fitness. For example, 'isodar analyses' (Morris 1987, 1988, 2003) can reveal deviations from ideal free distributions (Shochat et al. 2002) and only require that densities are measured repeatedly in two or more habitats. Examination of the 'habitat-matching rule' (Fagan 1987) can also reveal deviations from ideal distributions, but this method relies on measuring resource abundance in a variety of habitats (Johnson and Sherry 2001, Shochat et al. 2002), which is often difficult. Ornithologists should work to identify other practical techniques to evaluate how closely wild birds follow ideal distributions that do not require rigorous estimates of fitness.

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 Donazar (1996) found that habitat occupancy was related to both resource availability and reproduction for Imperial Eagles (*Aquila heliaca*) in Spain. This approach, which was followed by only 7% of the papers I reviewed, has the advantage that simple occupancy is usually far easier to quantify than intensive demographics, and it could be very useful for populations in heterogeneous landscapes and for which not all habitats are occupied every year. However, using temporal patterns of occupancy as a measure of habitat quality usually requires multiple seasons of data and can be clouded by changes in population size or landscape features. Moreover, site fidelity and social constraints or other forms of "time lags" (Wiens 1989b) can cause poor-quality habitats to remain occupied even when better habitats become available, decoupling the link between habitat occupancy and quality (Pulliam 2000). In addition, for birds whose home ranges encompass numerous patches of potentially very different habitats, it may be difficult to ascribe quality based on occupancy without understanding precisely which patches within the home range are most critical. Note that this discussion relates to temporal patterns in occupancy; examining spatial patterns of occupancy (e.g., "occupancy modeling" with

presence/absence analyses) is a form of use-availability habitat selection analysis (MacKenzie 2006), which is discussed above.

If birds distribute themselves among habitats with respect to their quality, habitats used for portions of the annual cycle should be inhabited in sequence from best to worst and abandoned from worst to best. Thus, arrival and departure dates in different habitats can be used as measures of habitat quality, especially for migratory birds (Alatalo et al. 1986, Marra 2000, Marra and Holmes 2001, Gunnarsson et al. 2006). For example, Lanyon and Thompson (1986) found that arrival patterns correlated with reproduction and habitat quality in Painted Buntings (*Passerina ciris*), and Smith and Moore (2005) confirmed that early-arriving American Redstarts chose the best habitats available and achieved higher reproductive output than later arrivals. This approach has the advantage of being easily measured for some systems (e.g., newly arriving and singing males), and arrival date can potentially reveal information relevant to the previous phase of the annual cycle (Gill et al. 2001, Norris 2005). However, this measurement may not be feasible for nonmigratory species showing strong site tenacity or little movement or for species with cryptic arrival and departure schedules. Perhaps as a result of these challenges, this technique has been relatively little used as a measure of habitat quality (2% of papers reviewed; Table 1). In addition, as with all distributional measures, the accuracy of this measurement as a metric of habitat quality is diminished if birds do not have adequate information on available habitats (Stamps et al. 2005), and recent work suggests birds may use each other as indicators of where to settle (Muller et al. 1997, Ahlering and Faaborg 2006), causing the initial settling period to be highly dynamic and not necessarily strongly associated with spatial variation in habitat quality.

Despotic 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 (*Den-*

droica occidentalis) and Townsend's (*D. 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. Approximately 6% of the papers reviewed used this measurement of habitat quality. This approach can be convenient for field studies, but it requires that dominant and subordinate individuals be easily distinguished (e.g., by age-specific plumage or body size) and relies on a well-established despotic distribution. Moreover, precisely when age ratios are determined is important, because postbreeding age ratios are often used as an index of reproduction, with the opposite prediction—the best (most productive) habitats should have a low ratio of adults:young (Flanders-Wanner et al. 2004, Peery et al. 2007).

Individual condition measures. Many of the measurements of habitat quality reviewed so far require measuring populations of birds, often over extended breeding or nonbreeding periods. These approaches 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 researchers have used measures of individual birds' physical condition as indicators of habitat quality (9% of papers reviewed).

We can distinguish variables that rely on external, visible, and measurable features, which I call morphological condition measures, from variables that rely on analysis of sampled tissues (especially blood), called physiological condition measures. Regardless, all measures of body condition share two requirements to be useful as indicators of habitat quality. First, variation in condition must be a consequence (rather than a cause) of differential habitat use. That is, variation in habitat attributes such as food supply and predation risk must lead to variation in physical condition. This may often be at least partially true, but in some systems it is also likely that preexisting differences in condition lead birds to use different habitats. 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. Second, using measures of body condition as indicators of habitat quality requires that differences in condition ultimately manifest in differential fitness. This has been confirmed in only a few species (Bêty et al. 2003, Johnson et al. 2006) and merits further study. Statistically significant variation in body condition among habitats does not guarantee variation in reproduction or survival.

It is also important for researchers to match the temporal scale over which measures of body condition change to the temporal scale over which habitat quality is sought to be judged. For example, analysis of induced feather growth (ptilochronology) has been used to reflect nutritional aspects of habitat quality for birds during the time it takes to regrow a feather with a sufficient number of growth bars for measurement (several weeks to months; Grubb 1989, Grubb and Yosef 1994). In contrast, body mass can change seasonally in response to fluctuations in environmental conditions such as habitat quality (Rintamäki et al. 2003), and plasma metabolites change hourly, reflecting the feeding and fasting behavior of birds occupying habitats over very short temporal "windows" (Jenni-Eiermann and Jenni 1994). This variation in measures of body condition over time both enhances and detracts from their capacity as indicators of habitat quality. On one hand, dynamic measures of body condition are potentially much more sensitive to variation in habitat quality than are more static measures, such as demographics, and they may enable biologists to quantify habitat quality for birds occupying habitats only briefly. On the other hand, these dynamic measures may be too subject to temporal fluctuation to reveal lasting variation in habitat quality. For example, fat stores in wintering songbirds may reveal more about recent weather patterns than about the quality of winter-occupied habitats (Rogers et al. 1994). Measures of body condition that change more slowly may be useful to rank habitats occupied for long periods, but for mobile species they may not reflect local habitat quality. For example, the condition of a migratory songbird at a stopover site may be more dependent on

the habitats it has occupied in the previous months than on its current habitat conditions (Bearhop et al. 2004). Researchers must seek to understand which periods of the season are most critical, and optimize their sampling of body condition accordingly.

Many different body condition measures have been considered indicators of habitat quality. Common morphological measures include changes in body mass (Pöysä et al. 2000), body size (often based on multiple morphometrics), mass corrected for body size (Latta and Faaborg 2002), fat stores (Strong and Sherry 2000, Brown et al. 2002), ptilochronology (Grubb and Yosef 1994, Carlson 1998), various measures of pigmentation (especially the prominence of ultraviolet wavelengths; Siefferman and Hill 2005), and fluctuating asymmetry (Lens et al. 1999), the latter based on the notion that high-quality habitats enable symmetrical morphological development. Physiological measures have been less commonly used, but endocrinological indicators of stress (e.g., concentrations of corticosterone in blood) have increasingly been used to assess habitat quality (Marra and Holberton 1998, Lanctot et al. 2003). Recently, workers have suggested that concentrations of blood plasma metabolites, especially triglycerides and β -hydroxy-butyrate (Jenni-Eiermann and Jenni 1994, Williams et al. 1999, Seaman et al. 2006), can indicate short-term patterns of foraging and fasting and thus provide a measure of habitat quality. With all of these measures, researchers should first confirm they indicate habitat quality as hypothesized by comparing measures in habitats known from independent work to be high and low in quality (Guglielmo et al. 2005).

RECOMMENDATIONS

Animal distribution is dependent upon the fitness conferred by selected habitats (Fretwell and Lucas 1970), which provides the theoretical underpinnings for conceptualizing and measuring habitat quality for birds (Block and Brennan 1993, Franklin et al. 2000). When we know what resources and ecological constraints govern fitness and can measure them, measuring habitat quality directly is advisable, but it is often impractical in field settings. Researchers and managers should resist the temptation to

use vegetation type as a crude surrogate for habitat quality.

When using habitat-specific measures of the abundance, performance, or condition of birds to reveal habitat quality, ecologists should emphasize demographics whenever feasible. This approach is appropriate because the root of habitat quality as a concept lies in demography (Block and Brennan 1993, Hall et al. 1997, Knutson et al. 2006), and demographic measurements suffer from few limitations except their difficulty to obtain. In addition, for managers to effect change for wild birds, they must work to identify on-the-ground variables that influence avian demography. However, reproduction, survival, and abundance may not all be positively correlated, which can lead to misleading indicators of habitat quality. In the past, researchers have too often measured only one parameter at a time (especially abundance or reproduction). To enable ecologists and managers to more successfully measure multiple demographic indicators of habitat quality, new methods and technologies should be developed to feasibly quantify previously elusive parameters for wild birds.

When quantifying variables related to the distribution of birds as measures of habitat quality (e.g., habitat selection or habitat occupancy), investigators should first investigate how closely their study species follow ideal distributions, because a variety of ecological factors can lead birds to select poor and avoid rich habitats, violating critical assumptions of all distributional measures. Resolving whether a given bird population more closely follows a free or despotic distribution will also determine whether density is likely to be correlated with fundamental habitat quality. To improve the reliability of distributional measures of habitat quality, ecologists need more approaches for assessing model assumptions that do not require measuring fitness.

Lastly, measures of body condition can provide convenient measures of habitat quality, and they offer exciting new methods to assess habitat quality, but the link between body condition and habitat-specific fitness has been confirmed in relatively few systems. Much work is needed to evaluate whether measures of body condition are as useful as distribution and demographics for indicating variation in avian habitat quality.

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