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Commentary

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Habitat Selection Studies in Avian Ecology: A Critical Review

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The study of habitat use and selection in birds has a long tradition (Grinnell 1917, Kendeigh 1945, Svärdson 1949, Hildén 1965; Block and Brennan 1993). Early habitat-selection theory was characterized by correlative models of habitat characteristics and species abundance (MacArthur and Pianka 1966, Verner et al. 1986, Rosenzweig 1991), which subsequently evolved into models that involved density dependence: the ''ideal-free distribution'' and ''ideal-despotic distribution'' models (Fretwell and Lucas 1970, Fretwell 1972). More recently, habitat-selection studies have shown that many factors, such as landscape structure, can influence exactly how ''ideal'' and ''free'' animals are while moving through a landscape and selecting habitats (Karr and Freemark 1983, Pulliam and Danielson 1991, Petit and Petit 1996).

Habitat-selection studies have recently assumed a new urgency, partially as a result of the importance of incorporating both habitat and demographic information into conservation planning (Caughley 1994). Nevertheless, ornithologists tend to be inconsistent in their conceptual framework and terminology with regard to (1) what constitutes habitat use versus selection, (2) the behavioral and evolutionary context of their findings, and (3) the order or scale of their study, from microhabitat to geographic range (Johnson 1980, Orians and Wittenberger 1991). The purpose of this review is to address those concerns through a survey of recent literature and highlight areas where improvements or advances can be made in avian habitat ecology.

Three Areas of Concern.—Definitions.—The semantic and empirical distinctions between the terms *habitat use* and *habitat selection* are often unclear (Hall et al. 1997). *Habitat* refers to a distinctive set of physical environmental factors that a species uses for its survival and reproduction (Block and Brennan 1993). *Habitat use* refers to the way in which an individual or species uses habitats to meet its life history needs (Block and Brennan 1993). The study of habitat-use patterns describes the actual distribution of individuals across habitat types (Hutto 1985). *Habitat selection* refers to a hierarchical process of behavioral responses that may result in the disproportionate use of habitats to influence survival and fitness of individuals (Hutto 1985, Block and Brennan 1993). *Habitat selection* carries a connotation of understanding complex behavioral and environmental processes that *habitat use* does not; habitat-use patterns are the end result of habitat-selection processes. *Nest-site selection* is a subset of habitat selection focusing solely on nest sites.

Context.—The ability of researchers to place their findings in an appropriate behavioral or evolutionary context varies widely. Much of that variation lies in researchers' ability to generate specific questions and to place the answers to those questions into broader theoretical frameworks. There are two aspects of habitat selection that are crucial to understanding the adaptive significance of disproportionate use of habitats; demonstration of choice and an assessment of the fitness consequences associated with the choice.

First, habitat selection is a decision-making process and researchers need to make an attempt to describe how the observed patterns reflect individual choice. That attempt can be improved by the recognition that individuals are faced with choices that differ not only in terms of habitat quality, but also in terms of the costs and benefits of acquiring space (Fretwell and Lucas 1970, Kennedy and Gray 1994).

Second, habitat preferences are assumed to be adaptive without demonstration of increased fitness in preferred habitats (Robertson 1972, Pulliam and Danielson 1991, Martin 1998). There is no guarantee that the presence of individuals in a given habitat is positively related to habitat quality (Van Horne 1983, Pulliam 1988, Caughley 1994). In the absence of behavioral or life-history information, there is no way to know if detected differences have any bearing on choices of individuals (Martin 1992, 1998).

In addition, many nonhabitat-related phenomena influence habitat selection in birds (Cody 1981, 1985), including nest predation (Sonerud 1985, Martin 1993), competition (Svärdson 1949, Martin 1993, Petit and Petit 1996), intraspecific attraction (Danchin et al. 1998, Forsman et al. 1998, Pöysä et al. 1998), and food limitation (Martin 1993, McCollin 1998). There needs to be explicit recognition of how

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those phenomena affect both the choices made by individuals and the fitness consequences of those choices.

Methodology.—The empirical and statistical methods by which habitat selection is inferred differ greatly in their precision and applicability (Alldredge and Ratti 1986, 1992). There are two main ways in which habitat selection is tested for breeding birds with territorial systems: comparing used habitats with unused habitat and comparing used habitats with available habitats. *Used* habitat is habitat currently occupied by the focal individual or species; *unused* habitat is not currently occupied. *Available* habitat refers to all habitat types in a prescribed area and includes habitats currently in use.

The used versus unused comparison is considered the less informative of the two methods (Johnson 1980). Information on the quality of used versus unused space is only informative about habitat selection if the unused habitat is actually available to the birds of interest. Further, absence from a particular habitat does not mean that the habitat is being avoided (Wiens 1989, Haila et al. 1996). Population density and demographics may have a major effect on which habitats are used or unused (Rotenberry and Wiens 1980, Wiens 1986, Wiens et al. 1987, Haila et al. 1996).

In addition, there are statistical issues concerning the comparison of used and unused areas. Of particular importance is the concern raised over statistical methods that fail to consider that an individual's use of a particular habitat affects its use of other habitats (Thomas and Taylor 1990, Aebischer et al. 1993). The lack of independence negatively affects the power of many of the statistical techniques used to analyze such proportional use (Alldredge and Ratti 1986, 1992; James and McCulloch 1990, Aebischer et al. 1993). Analytical techniques should test for departures from random use. If nonrandom use is detected, techniques should then assess which habitats are used more or less than expected by chance (Aebischer et al. 1993). Johnson's (1980) unit-sum constraint is an example of such a technique.

Used-versus-available tests involve comparisons of habitats currently used by individuals to habitats available to be used. Those comparisons are preferable to used-versus-unused comparisons because they allow researchers to make inferences about choice. However, the used-versus-available comparisons are also problematic in that the measurement of habitat availability is very difficult. First, availability refers to both the accessibility and procurability of resources, not just their abundance (Wiens 1984, Hall et al. 1997, Martin 1998). The definition of availability based solely on the proportional area of habitat types makes a rarely tested assumption that all parts of the study area are equally available (Kennedy and Gray 1994, Arthur et al. 1996, Spencer et al. 1996). In addition, many researchers assume that a random sampling of habitats estimates habitat availability, although that assumption is seldom tested in the field.

Second, both the spatial and temporal scales of the study influence the perception of habitat availability (Wiens 1973, Kotliar and Wiens 1990, Orians and Wittenberger 1991) and, hence, our sense of habitat selection (Clark and Shutler 1999). Johnson (1980) defined four orders of habitat selection that acknowledge its hierarchical nature and provide a useful empirical framework for habitat studies. Johnson's framework ranges from the macroscale descriptions of the geographical or physical range of a species (first-order selection) to microscale descriptions of the actual attainment of food items or selection of nest sites from those available (fourth-order selection). If the scale of study and analysis is not tailored to the species and question of interest, key influences on habitat selection may be missed by the research (Orians and Wittenberger 1991). For example, when examining habitat use within territories, the individual has likely already made a crucial selection by choosing a territory. Researchers should be explicit about the constraints that prior decisions made by the animal place on its current options (Johnson 1980).

Third, habitat availability often is not assessed in a manner relevant to the individual or species in question (Aebischer et al. 1993, Gates and Evans 1998). Available habitat is usually assessed within a study area, the boundaries of which are often arbitrarily drawn. A more accurate assessment of habitat availability is one that is informed by the natural- and life-history characteristics of the focal species. For example, when considering selection of habitat components from within territories or home ranges (third-order selection; *sensu* Johnson 1980), the measurement of habitat availability should be constrained by the boundaries of the territory or home range (Evans and Gates 1997, Gates and Evans 1998).

Methods.—I surveyed the last 14 years (1986 to 1999) of four North American ornithological journals—*The Auk, The Condor, Journal of Field Ornithology,* and *The Wilson Bulletin.* I considered the content of those four journals to be representative of the state of the avian research to date. I chose 1986 as the starting point because it was the first full publication year following the publication of *Habitat Selection in Birds,* (Cody 1985). I searched titles, abstracts, and key words for the terms habitat use, habitat characteristics, habitat associations, habitat selection, and nest-site selection. Papers were grouped into three exclusive categories: habitat-use papers, habitat-selection papers, and nest-site selection papers. Within each category, papers were classified according to the characteristics of both the research within each manuscript and how the research was presented. I asked several questions of each paper: (1) Were the authors consistent and accurate in their usage of habitat terminology throughout the paper? (2) If the paper ex-

amined habitat or nest-site selection, did the authors contrast used habitats with unused habitats or did they address habitat availability? (3) If the authors addressed habitat availability, did they define availability arbitrarily (e.g. within preset study area boundaries), or did they consider the ecology of the study system when designing their habitat sampling method (e.g. within territory boundaries when assessing nest-site selection)? (4) If the authors addressed habitat or nest-site selection, did they attempt to place their findings in a behavioral or fitness context?

I assessed whether or not the frequency of errors changed over time by grouping papers into the following time intervals: 1986 to 1989, 1990 to 1994, and 1995 to 1999. I compared the percentage of total papers committing semantic, methodological, and contextual, errors across each of the three time intervals using chi-square tests. Below, I deal with semantic concerns first because the papers that suffered from such concerns were not included in the assessment of methodological and contextual issues.

Results and Discussion.—In total, 185 papers were included in this review: 73 habitat use, 51 habitat selection, and 61 nest-site selection. Forty-two were published in the period 1986–1989, 56 during 1990–1994, and 87 during 1995–1999.

Semantics.—Overall, 24% (44/185) of the surveyed papers suffered from semantic inconsistencies. Problems ranged from using *habitat use* and *habitat selection* as synonyms (e.g. Darveau et al. 1992) to solely describing nest-site characteristics without reference as evidence of nest-site selection (e.g. Schaffner 1991). This study is not the first to raise concern over the lack of semantic standardization in the habitat field (Romesburg 1981, Morrison et al. 1992, Hall et al. 1997). That nearly one-quarter of the papers surveyed in this review misinterpreted or misused the terms habitat use, habitat selection and nest-site selection indicates that the problem remains pervasive in avian ecology. Further, the situation does not appear to be improving; there was no difference in the propensity for error across the three time periods ($\chi^2 = 3.05$, df = 184, $P = 0.22$). Why the problem remains is perhaps related to the commonness of the terminology; authors may assume that everybody knows what habitat selection is and, therefore, pay less attention to providing operational definitions when presenting their research. Although the avian habitat literature appears to have fewer semantic inconsistencies than other fields (Hall et al. 1997), researchers need to strive to insure that essential concepts are clearly defined if habitat ecology is to continue to develop and maintain its position as one of the central fields in avian research. The lack of semantic clarity carries over into the ability of researchers to develop a meaningful context surrounding their results.

Methodology.—Of the 141 papers without semantic concerns, 46% ($n = 65$) made empirical decisions that rendered many of the results difficult to interpret and, possibly, inaccurate. There was no difference in the propensity for error across the three time periods ($\chi^2 = 2.13$, df = 140, $P = 0.34$). Most of the reviewed papers that examined habitat selection described a used-versus-available comparison (76%) rather than a used-versus-unused comparison (24%), although the latter is widely used in wildlife management (White and Garrott 1990). Very few of the reviewed papers that employed used-versus -unused comparisons addressed issues of accessibility and availability. For example, Frederick and Gutiérrez (1992) tested habitat selection in White-tailed Ptarmigan (*Lagopus leucurus*) by restricting the location of unused sites to sites within regions of concentrated use, thereby guaranteeing habitat accessibility. Unless accessibility can be addressed, a better approach is to examine areas where birds are found and look at probability or frequency of usage across used areas (e.g. Anderson and Tacha 1999). Finally, few papers used statistical methodology designed to account for the nonindependence of proportional use of habitats (e.g. Ryan and Renkin 1987).

The majority of papers that actually examined habitat selection employed a form of the used-versus-available habitat comparison. Although that is encouraging, many researchers failed to explicitly recognize that not all habitats are equally available for use and did not structure their habitat sampling methodology accordingly. Less than half of the papers that employed a used-versus-available comparison to test habitat selection defined availability in a manner relevant to the species or individual in question. For example, when examining nest-site selection, many authors compared nest-site characteristics with habitat characteristics at random sites that were selected without reference to territory boundaries (e.g. Pampush and Anthony 1993, Linder and Anderson 1998). The assessment of habitat availability likely included habitat not available to the focal individual and, consequently, erroneous differences between nest-sites and available habitat could have been described. Constraining the assessment of habitat availability to within territory boundaries will provide a more accurate picture of nest-site or foraging site selection (e.g. Ramsay et al. 1999).

The issue of availability can be compounded when dealing with species having unique habitat requirements. Smith et al. (1999) documented nest-site selection by Great Horned Owls (*Bubo virginianus*), a species that requires nest structure built by other species. However, in their selection of random sites to document availability, they did not record the presence or absence of potential nest sites, such as old corvid nests. If there are no potential nest sites, the habitat is technically not available. On the other hand, Sieg and Becker (1990) provided a truer assessment of availability for Merlins (*Falco columbarius*), which also require nests built by heterospecifics,

by centering their nonnest habitat plots on unused Black-billed Magpie (*Pica pica*) nests.

Context.—Thirty-eight percent (46/121) of the papers that examined habitat or nest-site selection did not provide a behavioral or fitness context for their findings. There was no difference in the propensity for error across the three time periods ($\chi^2 = 0.32$, df = 120, $P = 0.85$). Given so many known nonenvironmental influences on habitat selection, it is perhaps troubling that over one-third of habitat selection papers neglected to acknowledge the potential effects of nonenvironmental factors on patterns they describe. Obviously, no single research project can cover all potential influences, but the existence of multiple constraints on individual behavior needs to be explicitly noted. For example, Hooge et al. (1999) focused their efforts in documenting nest-site selection by Acorn Woodpeckers (*Melanerpes formicavorus*) on the potential influence of microclimate on habitat selection, but expanded their discussion to include the role of nest predation. In contrast, Wilson et al. (1998) offer only a cursory explanation of observed patterns of habitat selection by peatland birds, which limits the ability of the reader to appreciate the historical dynamics of the system.

The results of this review indicate that few habitat and nest-site selection papers have addressed why the selection of certain habitats was adaptive for the species in question. One notable exception was Badyaev et al.'s (1996) examination of habitat selection in female Wild Turkeys (*Meleagris gallopavo*); not only did the authors examine the reproductive consequences of habitat selection by individuals, they documented the process by which females behaviorally sampled habitat availability.

Summary.—The results of my time-period analysis, coupled with the frequency of error detected in this review, indicate that my concerns regarding the general state of avian habitat selection research were valid. One concern was that ornithologists tend not to consistently evaluate the behavioral and fitness context of their findings. That can be ameliorated by recognizing that (1) habitat selection refers to a process and not a pattern, (2) that there are many extrinsic factors that influence habitat selection, and (3) that a complete test of habitat selection involves an assessment of whether or not the documented habitat preferences are adaptive. A second concern was that ornithologists do not consistently use and perceive habitat-related terminology. That lack of consistency can be remedied by providing operational definitions to limit misunderstanding. A third concern was that methodologies commonly employed to document habitat selection do not account for the hierarchical nature of habitat selection and do not generate accurate representations of habitat availability. Comparisons of used habitat with available habitat are more appropriate than comparisons of used and unused habitat. Definitions of habitat availability ought to be informed by the natural- and life-history characteristics of the focal species.

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Literature Cited

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Alldredge, J. R., and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 50:157–165.

Alldredge, J. R., and J. T. Ratti. 1992. Further comparison of some statistical techniques for analysis of resource selection. Journal of Wildlife Management 56:1–9.

Anderson, J. T., and T. C. Tacha. 1999. Habitat use by Masked Ducks along the Gulf Coast of Texas. Wilson Bulletin 111:119–121.

Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. Ecology 77:215–227.

Badyaev, A. V., T. E. Martin, and W. J. Etges. 1996. Habitat sampling and habitat selection by female Wild Turkeys: Ecological correlates and reproductive consequences. Auk 113:636–646.

Block, W. M., and L. A. Brennan. 1993. The habitat concept in ornithology: Theory and applications. Current Ornithology 11:35–91.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Clark, R. G., and D. Shutler. 1999. Avian habitat selection: Pattern from process in nest-site use by ducks? Ecology 80:272–287.

Cody, M. L. 1981. Habitat selection in birds: The roles of vegetation structure, competitors and productivity. BioScience 31:107–113.

Cody, M. L., Ed. 1985. Habitat Selection in Birds. Academic Press, New York.

Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: Implications for the study of coloniality. Ecology 79:2415–2428.

Darveau, M., J.-L. Desgranges, and G. Gauthier. 1992. Habitat use by three insectivorous birds in declining maple forests. Condor 94:72–82.

Evans, D. R., and J. E. Gates. 1997. Cowbird selection of breeding areas: The role of habitat and

bird species abundance. Wilson Bulletin 109: 470–480.

FORSMAN, J. T., M. MÖNKKÖNEN, P. HELLE, AND J. INKERÖINEN. 1998. Heterospecific attraction and food resources in migrants' breeding patch selection in northern boreal forest. Oecologia 115: 278–286.

FREDERICK, G. P., AND R. J. GUTIÉRREZ. 1992. Habitat use and population characteristics of the White-tailed Ptarmigan in the Sierra Nevada, California. Condor 94:889–902.

FRETWELL, S. D. 1972. Populations in Seasonal Environments. Princeton University Press, Princeton, New Jersey.

FRETWELL, S. D., AND H. L. LUCAS, JR. 1970. On territorial behavior and other factors influencing habitat distributions of birds. I. Acta Biotheoretica 19:16–36.

GATES, J. E., AND D. R. EVANS. 1998. Cowbirds breeding in the central Appalachians: Spatial and temporal patterns and habitat selection. Ecological Applications 8:27–40.

GRINNELL, J. 1917. Field tests of theories concerning distributional control. American Naturalist 51: 115–128.

HAILA, Y., A. O. NICHOLLS, I. K. HANSKI, AND S. RAIVIO. 1996. Stochasticity in bird habitat selection: Year-to-year changes in territory in a boreal forest birds assemblage. Oikos 76:536–552.

HALL, L. S., P. R. KRAUSMAN, AND M. L. MORRISON. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin 25: 173–182.

HILDÉN, O. 1965. Habitat selection in birds: A review. Annales Zoologici Fennici 2:53–75.

HOOGE, P. N., M. T. STANBACK, AND W. D. KOENIG. 1999. Nest-site selection in the Acorn Woodpecker. Auk 116:45–54.

HUTTO, R. L. 1985. Habitat selection by nonbreeding, migratory land birds. Pages 455–476 *in* Habitat Selection in Birds (M. L. Cody, Ed.). Academic Press, New York.

JAMES, F. C., AND C. E. MCCULLOCH. 1990. Multivariate analysis in ecology and systematics: Panacea or Pandora's Box. Annual Review of Ecology and Systematics 21:129–166.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

KARR, J. R., AND K. E. FREEMARK. 1983. Habitat selection and environmental gradients: Dynamics in the ''stable'' tropics. Ecology 64:1481–1494.

KENDEIGH, S. C. 1945. Community selection in birds on the Heldenberg Plateau of New York. Auk 62: 418–436.

KENNEDY, M., AND R. D. GRAY. 1994. Agonistic interactions and the distributions of foraging organisms: Individual costs and social information. Ethology 96:155–165.

KOTLIAR, N. B., AND J. A. WIENS. 1990. Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. Oikos 59:253–260.

LINDER, K. A., AND S. H. ANDERSON. 1998. Nesting habitat of Lewis' Woodpeckers in southeastern Wyoming. Journal of Field Ornithology 69:109–116.

MACARTHUR, R. H., AND E. R. PIANKA. 1966. On optimal use of a patchy environment. American Naturalist 100:603–609.

MARTIN, T. E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? Pages 455–473 *in* Ecology and Conservation of Neotropical Migrants (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.

MARTIN, T. E. 1993. Nest predation and nest sites: New perspectives on old patterns. BioScience 43: 523–532.

MARTIN, T. E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? Ecology 79:656–670.

MCCOLLIN, D. 1998. Forest edges and habitat selection in birds: A functional approach. Ecography 21:247–260.

MORRISON, M. L., B. G. MARCOT, AND R. W. MANNAN. 1992. Wildlife-habitat Relationships: Concepts and Applications. University of Wisconsin Press, Madison.

ORIANS, G. H., AND J. F. WITTENBERGER. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137(Supplement):29–49.

PAMPUSH, G. J., AND R. G. ANTHONY. 1993. Nest success, habitat utilization and nest-site selection of Long-billed Curlews in the Columbia Basin, Oregon. Condor 95:957–967.

PETIT, L. J., AND D. R. PETIT. 1996. Factors governing habitat selection by Prothonotary Warblers: Field tests of the Fretwell–Lucas models. Ecological Monographs 66:367–387.

PÖYSÄ, H., J. ELMBERG, K. SJÖBERG, AND P. NUMMI. 1998. Habitat selection rules in breeding Mallards (*Anas platyrhynchos*): A test of two competing hypotheses. Oecologia 114:283–287.

PULLIAM, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

PULLIAM, H. R., AND B. J. DANIELSON. 1991. Sources, sinks, and habitat selection: A landscape perspective on population dynamics. American Naturalist 137(Supplement):50–66.

RAMSAY, S. M., K. OTTER, AND L. M. RATCLIFFE. 1999. Nest-site selection by female Black-capped Chickadees: Settlement based on conspecific attraction. Auk 116:604–617.

ROBERTSON, R. J. 1972. Optimal niche space of the Red-winged Blackbird (*Agelaius phoenicus*). I. Nesting success in marsh and upland habitat. Canadian Journal of Zoology 50:247–263.

ROMESBURG, H. C. 1981. Wildlife science: Gaining reliable knowledge. Journal of Wildlife Management 45:293–313.

ROSENZWEIG, M. L. 1991. Habitat selection and population interactions: The search for mechanism. American Naturalist 137(Supplement):5–28.

ROTENBERRY, J. T., AND J. A. WIENS. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: A multivariate analysis. Ecology 61:1228–1250.

RYAN, M. R., AND R. B. RENKIN. 1987. Habitat use by breeding Willets in the northern Great Plains. Wilson Bulletin 99:175–189.

SCHAFFNER, F. C. 1991. Nest-site selection and nesting success of White-tailed Tropicbirds (*Phaethon lepturus*) at Cayo Luís Peña, Puerto Rico. Auk 108:911–922.

SIEG, C. H., AND D. M. BECKER. 1990. Nest-site habitat selected by Merlins in southeastern Montana. Condor 92:688–694.

SMITH, D. G., T. BOSAKOWSKI, AND A. DEVINE. 1999. Nest site selection by urban and rural Great Horned Owls in the northeast. Journal of Field Ornithology 70:535–542.

SONERUD, G. A. 1985. Nest hole shift in Tengmalm's Owl *Aegolius funereus* as defence against nest predation involving long-term memory in the predator. Journal of Animal Ecology 54:179–192.

SPENCER, H. G., M. KENNEDY, AND R. D. GRAY. 1996. Perceptual constraints on optimal foraging: The effects of variation among foragers. Evolutionary Ecology 10:331–339.

SVÄRDSON, G. 1949. Competition and habitat selection in birds. Oikos 1:157–174.

THOMAS, D. L., AND E. J. TAYLOR. 1990. Study designs and tests for comparing resource use and availability. Journal of Wildlife Management 54:322–330.

VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

VERNER, J., M. L. MORRISON, AND C. J. RALPH, EDS. 1986. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of Wildlife Radiotracking Data. Academic Press, San Diego, California.

WIENS, J. A. 1973. Pattern and process in grassland bird communities. Ecological Monographs 43: 237–270.

WIENS, J. A. 1984. Resource systems, populations, and communities. Pages 397–436 *in* A New Ecology: Novel Approaches to Interactive Systems (P. W. Price, C. N. Slobodchikoff, and W. S. Gaud, Eds.). John Wiley and Sons, New York.

WIENS, J. A. 1986. Spatial scale and temporal variation in studies of shrubsteppe birds. Pages 154–172 *in* Community Ecology (J. Diamond and T. J. Case, Eds.). Harper and Row, New York.

WIENS, J. A. 1989. The Ecology of Bird Communities, vol. 1. Foundations and Patterns. Cambridge University Press, New York.

WIENS, J. A., J. T. ROTENBERRY, AND B. VAN HORNE. 1987. Habitat occupancy patterns of North American shrubsteppe birds: The effects of spatial scale. Oikos 48:132–147.

WILSON, W. H., JR., R. E. ZIERZOW, AND A. R. SAVAGE. 1998. Habitat selection by peatland birds in a central Maine bog: The effects of scale and year. Journal of Field Ornithology 69:540–548.

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