



SPECIAL SECTION: CHOICES AND CONSEQUENCES OF AVIAN HABITAT SELECTION

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CHOICES AND CONSEQUENCES OF HABITAT SELECTION FOR BIRDS

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The collection of papers in this special section explores the premise that avian habitat ecology can be approached as an interaction between choices made by individuals and consequences of those choices (Jones 2001). This seemingly simple distinction between choices and consequences is emerging as a powerful unifying concept in avian habitat ecology. It allows a richer understanding of the behavioral process by which habitat choices are made, and links behavior to populations. It allows apparently pathological, maladaptive behaviors (such as use of ecological traps; reviewed by Battin 2004) to be understood simply as one point along a continuum of the same process that produces adaptive habitat choice, such as the ideal-free distribution (Fretwell and Lucas 1970), by allowing choices and consequences to be based on different habitat characteristics (Kristan 2003). For example, habitat choice can be based on distribution of food resources, whereas the reproductive consequences of this choice may be determined by predation (Shochat et al. 2005). It also allows synthesis of multiple scales of habitat variation, which can both inform birds' choices and bear consequences for their fitness at different stages in an annual cycle.

A choice of habitat at first glance seems to be similar to a foraging decision, but the two differ notably in the speed with which individuals are able to judge the accuracy of their decisions. Optimal foraging theory, for example, relates choice of foraging patch to some measure of fitness, usually expressed in terms of energy gain, and this approach has been very successfully applied to understanding distributions and population dynamics of foraging birds (Stillman et al. 2000). A principal lesson of optimal foraging studies is that birds make sensible choices among available foraging patches, limited by individual variation in competitive ability and information availability. Feedback about the accuracy of a foraging decision is received promptly because changes in foraging rates and satiation happen rapidly, and birds can adjust their foraging behavior quickly in response to poor choices (e.g., leave a patch with low resource levels). In contrast, there is intrinsically less information for the selection of habitat for other purposes, such as breeding, and there will often be time lags between the time when a choice is made and the time when the consequences of the choice are realized (Orians and Wittenberger 1991). The information available to individuals when they choose breeding habitat may consist of past experiences and current cues about habitat quality (e.g., conspecifics, predators, or vegetation), but future conditions that determine the success or

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failure of a breeding attempt cannot be observed directly. Changes in food levels (Blondel et al. 1993) and predator distributions (Söderström 2001) can only be forecast at the time when choices are made. In some cases birds may use “public information” from other birds already occupying a habitat to inform habitat choices (Ahlering and Faaborg 2006). To understand habitat ecology fully, we need to understand how habitats are selected, what determines habitat quality, how selection and quality interact, and over what time frame this interaction occurs.

The first two papers in this collection, by Johnson (2007) and Kristan (2007), explore the basic components of this problem. Johnson (2007) discusses ways to examine consequences of habitat occupancy by reviewing the literature on measuring habitat quality. With Wiens’s (1989) definition of habitat quality as the “fitness potential” of a habitat, he shows that there are many different ways to measure habitat quality, including demographic, physiological, and behavioral approaches. Although demographic approaches are the most directly related to a fitness-based definition of habitat quality, difficulties in measuring demographic rates in wild populations limit their use. Given this, he gives examples of how other approaches have been used, and discusses the strengths and weaknesses of each. Kristan (2007) presents a simple model that demonstrates how the interaction between habitat choice and population-level distribution and growth rate can be affected by changes in the multivariate structure of habitat. Additionally, he shows that optimal choice of habitat for one component of fitness can lead to poor habitat choices, and produce ecological traps, when correlations between habitat variables do not allow all components of fitness to be maximized simultaneously.

In spite of the need for birds to rely on cues for selecting habitat, habitat ecologists have assumed that choice of habitat should reflect habitat quality (Jones 2001). When the relationship between the attractiveness of habitat and its quality has been measured, habitat preferences have frequently shown the expected positive relationship with habitat quality (Martin 1998, Sergio and Newton 2003, Zimmerman et al. 2003). However, it has also been found that potentially important determinants of

fitness such as predation risk may not be predictable (Doran and Holmes 2005), or that the deleterious effects of novel alterations to habitat such as invasive plants may not be recognized (Lloyd and Martin 2005, Shochat et al. 2005). These problems are all potentially experienced by birds in urbanizing landscapes, a topic that is explored by Marzluff et al. (2007) in this collection. Urbanizing landscapes are composed of a mixture of natural and anthropogenic habitats, as well as native and non-native predators. Birds selecting habitat in such landscapes face a complex problem, in that the rich predator fauna is composed of species with different habitat associations and with the ability to move in response to breeding bird nesting densities. Predictability of habitat quality may be scale-dependent, thus habitat choice may be focused on only those scales that provide reliable information. Marzluff et al. (2007) found that the distribution of nest predators influenced the distribution of prey in a scale-dependent manner. Although nest predation was a major cause of nest failure, predator distributions were only associated with prey distributions at small scales, and for only some predators (principally Steller’s Jays [*Cynaocitta stelleri*]).

Understanding the intricacies of habitat selection becomes more difficult in migratory species. Norris and Marra (2007) point out that little is known about the “migratory connectivity” between wintering and breeding habitats, yet choices in one season can have influential demographic consequences in another time and place. Moreover, consequences of habitat choice in one season may constrain choices in the next by affecting preparation for and speed of migration. This clearly makes consequences of habitat choices difficult to trace, but it also underscores the necessity of examining relationships between habitat quality and demography in all phases of the annual cycle.

Empirical studies and theoretical treatments of habitat selection have been strongly influenced by the seminal work of Fretwell and Lucas (1970) on optimal habitat selection. Rather than choosing between good and poor habitats for breeding sites, however, birds may choose between establishing a breeding territory in poor habitat and becoming a nonbreeding “floater.” Brown and Long (2007) discuss floating as an alternative strategy, and tie

floating behavior to hormone levels involved in agonistic territorial interactions. Elevated corticosterone is found in individuals that lose agonistic interactions, and has been linked to greater incidence of nomadic behavior in lizards (*Urosaurus ornatus*; Knapp et al. 2003). Brown and Long (2007) raise the interesting possibility that floating is a side effect of losing agonistic interactions, and may thus be a correlated behavior that is not necessarily an adaptive choice.

Finally, an empirical study shows the potential benefits of studying avian habitat ecology as an interaction between choices and consequences. Seamans and Gutiérrez (2007) studied dispersal decisions in breeding Spotted Owls (*Strix occidentalis*), and show that choices to leave territories were affected by anthropogenic habitat alteration. Although individuals tended to choose the best available habitat when they dispersed, they only improved the quality of their territories approximately half of the time. Unpaired individuals were more likely to disperse than members of pairs, and pairing rates were higher after than before dispersal, suggesting that social factors may be more important than habitat quality for dispersing Spotted Owls.

The diversity of topics covered in this special section provides an overview of the benefits we expect to obtain from treating habitat ecology as an interplay between habitat choices and consequences. This approach promises to improve our understanding of the process of habitat selection and how it affects population distribution, abundance, and dynamics. Approaching habitat ecology in this way will encourage us to identify the times of year when habitat choices are made, the information that is available to birds and used at that time, and the individual fitness and population consequences of those choices.

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