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Scale and Context in Habitat Use and Selection during Avian Migration

Migratory birds travel extensively between breeding and non-breeding habitat to take advantage of seasonally-available resources. While distance and strategy vary by species and between populations, most passerines alternate periods of flight with a 'stopover' period of resting and intense foraging (Bairlein and Gwinner 1994). Upon arrival, birds are faced with the challenge of quickly finding suitable habitat in what are likely unfamiliar surroundings. Stopover habitat is important because the majority of the time during migration is spent at these locations and flight only makes a small proportion of the time (Hedenstrom and Alerstam 1997). Multiple factors may determine how long a bird stays at a stopover site including habitat availability, weather, and body condition (Bailein and Gwinner 1994). The ability to successfully forage between flights ultimately determines the success or failure of the journey.

Jones (2001) defined habitat use as the distribution of a species across habitat types and habitat selection as a hierarchical process in which an organism uses certain habitats over others. According to habitat selection theory, a fitness benefit or cost should be the result of this decision (Jones 2001). While numerous studies have explored habitat use and selection in birds during the breeding season (reviewed in Jones 2001), more recently stopover habitat selection has been the subject of several studies (reviewed in Deppe and Rotenberry 2008). The majority of these studies have focused on a single spatial scale. In one example, Rodewald and Brittingham (2004) explored habitat associations for five habitat types during fall migration. Using transect data to estimate bird abundance and species diversity, they found that most of the species (in which they had a large enough sample size) showed differences in association among the habitat types. The authors stated that landscape-level factors, which were not measured, could have had some influence on their results (Rodewald and Brittingham 2004).

Factors that influence habitat selection are dependent upon spatial scale (Orians and Wittenburger 1991). The choice of appropriate scale is dependent upon the species and the question of interest (Turner 1989, Wiens 1989, Levin 1992). Because a multi-scaled approach to understanding habitat selection could lead to increased understanding of different factors that influence habitat selection, several recent studies have examined stopover habitat use with multiple spatial scales. Buler et al. (2007) found that while weather and distance to the coast were important at a regional level, their results supported others who had found that overall food availability was the most important factor in understanding habitat selection. These results appear to agree with Moore and Aborn (2000) who stated that at a finer spatial scale intrinsic habitat characteristics may be more important than at a broader spatial scale. Other factors, such as weather, could affect habitat selection at the wider scale. Deppe and Rotenberry (2008) studied stopover habitat associations in the Yucatan peninsula, and found that for several species, associations differed depending upon a fine or broad spatial scale. In contrast, Tietz and Johnson (2007) did not find significant habitat associations between two forest types in California at either of two spatial scales: within study area and within home-range. Although they did find that within a habitat (microsite selection), 'lean' birds were found in locations with higher amounts of fruit than 'fat' birds (Tietz and Johnson 2007).

Ktitorov et al. (2008) found that landscape context was important in understanding stopover habitat use. Using multiple banding stations in Europe, the authors determined habitat cover at five spatial scales (1-5 km) surrounding a stopover site, and found that levels of habitat cover at three and five kilometers (depending upon species) were related to rates of mass gain (measured from banding data) (Ktitorov 2008). Based upon the results from the previous studies, a multi-scaled approach would continue to be an appropriate choice for future studies involving stopover habitat selection.

An example where different factors could be working at different spatial scales is for habitat selection on coastal islands along the eastern United States. One such location is Block Island, an island 15.5 km south of the southern Rhode Island coast. This is an important location for waves of migrating songbirds in the fall, who reach the island because of a 'coastal drift' effect from cold fronts with west winds (Ralph 1981). Previous research on the island has shown that numerous birds forage in the maritime shrubland habitat on the north end of the island which abundant with fruit (Parrish 1997, 2000, Smith et al. 2007). The maritime shrubland habitat is widespread throughout the island. Able (1977) found that large numbers of birds leave the island heading northeast, presumably back to the mainland at the closest point. This could provide an interesting study system, because it would appear that proximity to the mainland is important on a broad spatial scale in determining selection while other factors such as fruit abundance or plant species composition could be important on a finer scale. In summary, a careful understanding of the impact of scale on factors affecting habitat selection requires knowledge of the life history of the study species and multi-scaled approach.

Literature Cited (not included in Annotated Bibliography)

Able, K.P. 1977. The orientation of passerine migrants following offshore drift. Auk 94:320-330.

Bairlein, F. and E. Gwinner. 1994. Nutritional mechanisms and temporal control of migratory energy accumulation in birds. Annual Reviews in Nutrition 14:187-215.

Hedenstrom, A. and T. Alerstam. 1997. Optimum fuel load in migratory birds: distinguishing between time and energy minimization. Journal of Theoretical Biology 189:227-234.

Moore, F.R. and D.A. Aborn. 2000. Mechanisms of *en route* habitat selection: how do migrants make habitat decisions during stopover? Studies in Avian Biology 20:34-42.

Parrish, J.D. 1997. Patterns of frugivory and energetic condition in neartic landbirds during autumn migration. Condor 99:681-697.

Smith, S.B., K.H. McPherson, J.M. Backer, B.J. Pierce, D.W. Podlesak, and S.R. McWilliams 2007b. Fruit quality and consumption by songbirds during autumn migration. The Wilson Journal of Ornithology 119:419-428.

Tuner, M.G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics 20:171-97.

Annotated Bibliography

Buler. J.J., F.R. Mooore, and S. Woltmann. 2007. A multi-scale examination of stopover habitat use by birds. Ecology 88:1789-1802.

Habitat selection by migrating birds near the gulf coast was explored in this paper. The authors identified that food availability has been identified as the most important intrinsic factor in determining stopover habitat selection in migrating birds, but this is problematic because most supporting studies have explored selection at only a single spatial scale. This method prevents an understanding of the importance of factors extrinsic to food availability in habitat selection such as weather conditions and distance of the habitat from the coast (context). The author's compared bird abundance data to factors at three spatial scales: regional (proximity to the coast), landscape (amount of hardwood cover) and local (arthropod abundance and plant community composition). From the results of a principle components analysis they were able to determine that factors at the regional scale (sites closer to the coast were important in certain conditions) were important, but that food availability was ultimately the biggest determining factor in habitat selection.

Boyce, M.S. 2006. Scale for resource selection functions. Diversity and Distributions 12:269-276.

This article emphasizes the importance of carefully considering spatial and temporal scaling when modeling habitat selection using resource selection functions. The authors cite examples considering grain (resolution) and extent (domain) in determining habitat selection and species interactions. Resource selection functions can be used in a wide variety of applications including predicting abundance, diversity, and overlap of ranges for multiple species. The authors describe the influence of temporal scale (for example: between seasons, and also over multiple years). This article is an effective summary of the issues to be aware of when thinking about scale and habitat selections, and also provides examples of applications using resource selections functions.

Deppe, J.L. and J.T. Rotenberry. 2008. Scale-dependent habitat use by fall migratory birds: vegetation structure, floristics, and geography. Ecological Monographs 78:461-87.

The study examined habitat associations at two spatial scales for fall-migrating birds in the Yucatan peninsula. Using multiple spatial scales and a tropical study system, the authors wanted to evaluate the importance of vegetation architecture in explaining habitat associations. Given that plant species composition will likely change as migratory birds travel from breeding to non-breeding habitat, vegetation architecture could be a more important factor in explaining habitat associations than species composition. Using vegetation data and bird abundance and distribution data (from mist-netting and point counts), the authors found that habitat associations with vegetation structure varied by species depending upon scale. It was interesting that an association with certain vegetation metrics could show opposite results depending upon a broad or fine spatial scale, and highlights the importance of multi-scaled approaches to understanding habitat selection.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118:557-562.

This article gives a summary of habitat selection studies and highlights a few concerns to help guide future directions and study designs. The author begins by explicitly defining habitat use (distribution of animals across habitat types) and habitat selection (hierarchical decision-making process that could result in disproportionate habitat-use). As he stated, it becomes clear when reading numerous habitat selection articles that these terms are often used interchangeably. With regard to methodology, the author emphasized a need for understanding that multiple orders of habitat selection exist and that scale at which the study is designed needs to be based upon the question that is being examined and requires an understanding of the constraints that higher-order selection could have upon the scale explored in the study. Ideally, the scale used in a study should be explicitly stated, including the reasoning behind that decision. One other take-home message from this paper was that most studies have only used a single spatial scale, and that multiple scales create a better understanding of habitat selection.

Ktitorov, P., F. Bairlein, and M. Dubinin. 2008. The importance of landscape context for songbirds on migration: body mass gain is related to habitat cover. Landscape Ecology 23:169-179.

This goal of this study was to determine how the amount of surrounding suitable habitat at a stopover location influenced refueling rates. During fall migration in Europe, surrounding habitat cover at a banding station was divided into five spatial classes (1-5 km) and refueling rates were determined from capture data for two passerine species. The authors found that the amount of habitat cover in the three or five km distance classes (depending upon species) related to the mass gain. This result indicated the importance of landscape context (amount of surrounding habitat at a broader spatial scale) in determining refueling rates.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

This paper provides an extensive overview (theory and examples) of the importance of considering scale in ecology. Some important concepts include that understanding variability and predictability are entirely dependent upon the scale of study, and that multiple scales (ex. spatial and temporal) need to be used to gain a thorough understanding (including mechanism) of how process influences pattern. The following is cited within to Whitaker (1975), "the individualistic nature of responses to environment means that what we call a community or ecosystem is just really an arbitrary subdivision of a continuous gradation of local species assemblages (p. 1962)", and highlights the concept that there is no single correct scale at which to study a landscape, etc. This paper provides a basis for the idea that multi-scale studies could be the most informative.

Mayor, S.J., J.A. Schaefer, D.C. Schneider, and S.P. Mahoney. 2009. The spatial structure of habitat selection: a caribou's-eye-view. Acta Oecologica 35:253-260.

This study is obviously not about avian migration, but provides an example of a study in which multiple scales were determined by the movement patterns of the animal and spatial statistics, and not an arbitrary designation. In this study, habitat selection of caribou in Canada is described using four spatial scales. Two highlights from their introduction are that: 1.) habitat associations are scale-dependent and should be studied at multiple scales, 2.) habitat selection is hierarchical based upon the idea that selection of habitat at a broader scale constrains selection at a finer scale. A main point in the justification of design of their experiment was that arbitrarily-defining spatial scale limits interpretation of results and comparison with other studies. The behavior of the study species should define the ranges of the different selection scales. With the use of variograms and multivariate statistics (including principle components analysis), the authors use an organism-centered approach to understand behavior and habitat descriptions along a spatial continuum to define hierarchical classes of habitat selection. From the using change in variance to determine levels of habitat selection (and that variance decreases from a broader to finer spatial scale), the authors were able to determine that for this caribou population lichens and snow conditions were important in habitat selection.

Orians, G.H. and J.F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist (supplement) 137:S29-S49.

This is a study that focuses on breeding habitat selection (of Yellow-headed Blackbirds) in Washington and includes spatial and temporal scales in habitat selection. The theory supporting this study was clearly and concisely explained. The authors point out that when selecting a habitat, there is likely a benefit in deciding more quickly, but will result in decision-making with incomplete information. In the case of nest-site selection (probably more so than stopover habitat selection) the animal must make a prediction about future food availability. When Yellow-headed blackbirds are choosing their nesting habitat, odonates (the main food source for nestlings) have not emerged yet, so the adults have to predict where areas of odonate emergence will be highest. The authors found that food availability at the level of individual territories was not as important as availability at the broader scale (an entire marsh). Understanding of habitat selection in this study was directly linked to a detailed description and understanding of the life history traits of the species.

Rodewald, P.G. and M.C. Brittingham. 2004. Stopover habitat of landbirds during fall: use of edge-dominated and early-successional forest. Auk 121:1040-1055.

The goals of this study were to: 1.) compare habitat use in five different habitat types, 2.) compare multiple measures of vegetation (including fruit availability) between the habitat types, and 3.) explore differences in breeding versus stopover habitat type preferences for individual species and foraging guilds. They found that overall edge-dominated and early successional forests had the highest bird abundance and that use varied by habitat for 15 (of 21) species analyzed. Also, birds that bred in mature forested habitat used a wider array of habitat types during migration than bird that bred in shrub-type habitats. In their discussion, the authors acknowledged that landscape-level factors such as context and relative habitat availability could influence habitat preferences. The results from the within-habitat vegetation measures support the idea that structurally-heterogeneous habitat is preferred (at least for mature-forest breeding migrants).

Simons, T.R., S.M. Pearson, and F.R. Moore. 2000. Application of spatial models to the stopover ecology of trans-gulf migrants. Studies in Avian Biology 20:4-14.

This article discusses the use of landscape level variables with spatial modeling to understand habitat selection during stopover. Two types of models included are window analysis and individual-based analysis, and these models both use an index of energetic condition as a parameter in the model. The multiple parameters including weather and conditions allow more sensitive predictions of habitat use. These models could be useful in determining amounts of suitable habitat available.

Tietz, J.R. and M.D. Johnson. 2007. Stopover ecology and habitat selection of juvenile Swainson’s thrushes during fall migration along the northern California coast. Condor 109:795-807.

In this study, the authors used radio-tagged Swainson’s Thrushes caught along dune habitat to determine forest type selection at two spatial scales. They did not find any significant forest type selection within the study area (2^{nd} order) or within the birds’ home ranges (3^{rd} order selection), despite the forest types being quite different (broad-leaf vs. coniferous). These findings do not agree with several recent studies that found that certain habitats were preferred disproportionately to availability. The only differences they found were between fat and lean birds in micro-site selection; with fruit abundance (huckleberries) higher in locations of the lean birds.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

This paper is an effective introduction to the issue spatial scaling in ecology. The author concisely explains the importance of extent and grain in spatial variation. Fig. 2 shows how as grain increases variation decreases, and as extent increases variation between-grain may increase. The power of predictability depending upon the interaction between spatial and temporal scale is also explained in the paper. Again, as in other papers, the appropriate scale depends upon the question of interest. Also, the author explains some methods for choosing a scale that is not arbitrary, including using spatial statistics and the idea that variance increases as a domain of scale is approached.