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Abstracts

SPECIAL SECTION: HIERARCHICAL MODELS IN AVIAN ECOLOGY

HIERARCHICAL MODELS FOR AVIAN ECOLOGISTS

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As spatial ecology, biogeography, and landscape ecology progress we are increasingly aware of how spatial and temporal scale structure ecological patterns and affect ecological processes (Wiens 1989). Advances in these fields have come from studies of a variety of taxa, particularly plants and insects (With 1994, Ludwig and Tongway 1995, Wondzell et al. 1996, McIntyre and Wiens 1999, Östman and Ives 2003), but avian studies have also been influential and compelling. Scale dependence is found in bird movement patterns (Fritz et al. 2003), foraging ecology (Hinsley 2000), and habitat associations (Cushman and McGarigal 2002). The models we use to understand ecological systems should be compatible with the structure of the systems themselves (Maurer 2002), thus scale-dependent patterns should be explicitly explored.

This special section was inspired by a symposium on hierarchical approaches to studying avian ecology at the 2004 Cooper Ornithological Society meeting in La Crosse, WI. The La Crosse symposium, in turn, was inspired by the publication of Scott et al. (2002) "Predicting Species Occurrences: Issues of Accuracy and Scale." This compendium of concepts and methods for predicting species occurrence contained many exciting, promising advances in the art and science of modeling bird-habitat associations. It also contained disconcerting signs that we are not yet adequately dealing with the ecological and statistical problems that face us in this field. The first sign of trouble is that although habitat models are sometimes impressively predictive, often they are not (Wiens 2002). Predictive inaccuracy is a complex issue that conflates biological, methodological, and statistical problems, but predictive accuracy is a gold standard in science and the poor predictive power of habitat models is cause for concern. We currently have a vast array of statistical approaches available to apply to habitat modeling, including approaches that have only recently been practical due to heavy computational requirements (Stauffer 2002). Unfortunately, it is not clear that lack of statistical complexity or sophistication is the root of the problem (Huston 2002). Although technical advances may improve our ability to sample animals in the field, and to apply complex statistical models to their habitat associations, the greater need is to appropriately match statistical approaches with ecological structure (Maurer 2002, O'Connor 2002). It is natural, in light of this need, to explore the use of hierarchical statistical models in avian ecology.

The first paper in this special section points out that although "scale-dependent" is not synonymous with "hierarchical", there are reasons to suspect that hierarchical patterns should be common both in habitats and in bird responses to habitats (Kristan 2006). Hierarchical structure arises when variables can be considered components of other variables, and in turn to be made up of other component variables (O'Neill et al. 1986). A familiar type of hierarchy is a "nested" hierarchy, in which levels of one variable are completely contained within levels of another variable. The benefits of using hierarchical models include both statistical and conceptual gains. Statistical benefits arise from the fact that data that are hierarchically structured contain correlations between levels in the hierarchy, called "intraclass" correlations, that must be accounted for (Hox 1995, Goldstein 2003). Failing to account for intraclass correlation leads to underestimates of standard errors, because similarities among observations within a hierarchical level leads to lack of independence of observations and an artificially inflated sample size (Hox 1995, Goldstein 2003). One possible treatment of this statistical problem is to aggregate data to a higher level of organization (for example, averaging counts among areal units, such as census blocs or counties), because doing so can eliminate a level in the hierarchy, thereby eliminating one or more intraclass correlations. However, this may introduce problems in biological interpretation, because there is no guarantee that the relationships among variables at coarser levels of aggregation are the same strength, or even direction, as among individual observations. This problem is well known, and versions of it are known as the "ecological fallacy" by social scientists (King 1997, Goldstein 2003), and the "modifiable areal unit problem" (or the MAUP) by geographers and ecologists (Svancara et al. 2002). Maintaining information at all levels in the hierarchy allows patterns at different levels of aggregation to be explored, which could prevent serious misapplications of models. In predictive habitat modeling, for example, there is growing appreciation for the need to match the scale at which accuracy is assessed with the scale at which predictions are made; generally, coarse-scale predictions are more accurate than fine-scale predictions. This leads to a natural inclination to build and test models at the coarsest scale possible, and if there is good concordance between fine-scale and coarse-scale model predictions, then coarse-scale models may be preferred. If, however, fine and coarse scales of aggregation lead to different, conflicting predictions then both levels need to be considered.

The benefits to avian ecology of using hierarchical methods are compelling. We know that bird distributions can be modeled at coarse, geographic scales with climatic variables (Thomas and Lennon 1999), at intermediate scales by patch metrics (such as configuration and composition; McGarigal and McComb 1995), and at fine scales by traditional measures of habitat within 0.04-ha circular plots (James 1971). Furthermore, although we know that there are correlations among these levels, we also frequently find independent contributions of each level to overall patterns of occurrence (Knick and Rotenberry 1995, Howell et al. 2000). Our task is not to determine which scale is the correct one, but rather to determine how multiple scales of variation combine to produce the patterns of distribution and abundance that we observe. Hierarchical models may be appropriate tools for understanding how multiple spatial scales of variation in habitat lead to observed patterns of bird-habitat associations.

One lesson of the Scott et al. (2002) compendium is that there is no single method that will solve all problems in habitat modeling. Although we concentrated on hierarchical statistical approaches in the La Crosse symposium, we did not expect these methods to be a "technological fix." Rather, we wanted to explore how ornithologists are dealing with hierarchical structure in their data sets, and unsurprisingly there are several possible approaches. Link et al. (2006) used a hierarchical approach to model trends in American Black Duck abundance using Markov chain Monte Carlo models, in which the hierarchical structure resulted from nested route-level and observer-level effects. Thogmartin et al. (2006) used similar models, along with hierarchically structured habitat measures, to model grassland bird distributions across the upper midwestern

U.S. Although Link et al. (2006), and Thogmartin et al. (2006) both use the Markov chain Monte Carlo approach as a fitting algorithm, their basic model structure is a generalized linear model, which predicted abundance with linear functions of independent variables. Other approaches, such as niche envelope approaches, have been advocated by O'Connor and others (O'Connor 2002), and are also being applied to hierarchical analysis (Lawler and Edwards 2006).

In addition to the statistical problems raised by multiscale correlations, the ecological consequences of intraclass correlations are of interest. If birds sequentially select habitat variables at different levels of a hierarchy, then information that is correlated across spatial scales is essentially treated by the bird as part of the scale that is sampled first. Therefore, an investigator's perception of the importance of a level in the hierarchy to a bird-habitat association depends on whether it is assumed that birds select habitat based on fine-scaled features first (in which case the correlation between fine- and coarse-scaled features is interpreted entirely as an effect of the fine-scaled feature) or coarse-scaled features first (in which case the correlation between fine- and coarse-scaled features is interpreted entirely as an effect of the coarse-scaled feature). Lawler and Edwards (2006) explored this issue explicitly using a variance partitioning approach to measure the importance of cross-scale correlations in a multiscale habitat data set. Battin and Lawler (2006) discuss the design and sampling issues raised by the presence of cross-scale correlations in ecological data.

Although the papers presented here cover only a sampling of the possible methods for studying avian ecology, they all employ methods to better represent a common feature of ecological data sets. The potential to incorporate both hierarchical sampling variation and hierarchical habitat structure should make these techniques applicable to a variety of problems in avian ecology.