ANYTHING BUT BARREN, PART II: THE SEARCH FOR PATTERNS CONTINUES

by David C. Morimoto

In the April 1992 issue of *Bird Observer* (Morimoto 1992), I related preliminary results from a three-year study of the breeding bird community of the southeastern Massachusetts pine barrens. Thirty-one species were detected on eight sites that had been burned from fewer than five to more than thirty years prior to the onset of the study. Some species responded to the ecological differences among the sites, but many species exhibited few patterns. Although interspecific competition did not seem to be important, a complex picture of community structure was emerging, with species responding to habitat variation in different ways and to varying degrees.

Focusing the Search for Patterns. Following my initial work, I turned my attention to a more detailed study of Rufous-sided Towhees, Common Yellowthroats, and Prairie Warblers, each of which had exhibited intriguingly different patterns despite the fact that they were the most widespread and abundant species, comprising the bulk of the bird community (forty-nine to seventy percent of total density). Prairie Warblers exhibited strong habitat preferences, avoiding areas with higher tree coverage, whereas the superabundant towhees and yellowthroats exhibited only weak preferences. From these patterns I hypothesized that towhees and yellowthroats were responding to habitat characteristics in a way quite different from Prairie Warblers. Perhaps Prairie Warblers were far more sensitive to habitat characteristics than either the yellowthroat or the towhee.

Dispersion Patterns. To explore this hypothesis, I looked at the distribution of individuals of each of these species both within plots and among plots (Morimoto and Wasserman 1991a). By looking at different sized plots, I could determine differences among the species in what ecologists refer to as "scale." For example, at any given scale, individuals could exhibit one of three patterns of dispersion: random, even, or clumped (patchy). If the distribution patterns of the three species changed in different ways with changes in plot scale, and if these patterns were related to habitat variation, then there would be strong support for the hypothesis that each species responds to habitat in an individualistic, scale-specific manner. This analysis is analogous to looking at the dispersion patterns of people on a series of crowded coastal beaches on a hot summer day. At a fine scale of resolution corresponding to the size of individual people, one might detect a patchy dispersion as people would be clumped in family groups and other aggregates. At a coarser or larger scale (e.g., corresponding to the average group size) one might detect a pattern of even dispersion caused by the territorial nature of humans on beaches. At a still coarser scale (e.g., corresponding to an entire beach) one might again detect

patchy dispersion, as people would be grouped more densely on the higher quality beaches. Birdwatchers, on the other hand, would exhibit markedly different patterns of distribution (or, as ecologists like to call it, "dispersion"), being concentrated on relatively uninhabited beaches (unless a rarity happened to show up on a popular crowded beach).

All three bird species exhibited evenly spaced patterns within plots (analogous to a within-beach dispersion), clearly reflecting the territoriality resulting from intraspecific competition. This pattern held for Prairie Warblers even on plots where they were not very abundant, suggesting that they were selecting favorable patches of habitat within these plots.

When I looked at dispersion patterns across all plots at scales of resolution ranging from 0.25-0.50 hectares (roughly 0.6-1.25 acres and roughly equivalent to individual territory size) up to 7.0 hectares (roughly 17.75 acres and the size of entire plots), I found that all three species were evenly dispersed at smaller scales, consistent with the results of the within-plot analysis. However, Prairie Warblers became significantly clumped at scale sizes of 3.5 and 7.0 hectares, while Rufous-sided Towhees and Common Yellowthroats were randomly distributed at these coarser levels of resolution. This pattern held for each of the three years of the study. This result, combined with the results of the analysis of habitat associations, gave strong support to the hypothesis that the three species were responding at different scales to habitat variation. Prairie Warblers clearly responded to the structural differences in the various successional stages encompassed by my study, whereas Rufous-sided Towhees and Common Yellowthroats did not. The latter two species seemed to prefer equally well the entire array of pine barrens habitats included in this study.

These results are consistent with a belief that bird communities are composed of individuals having their own species-specific "ecological neighborhoods" (Addicott et al. 1987) or "patch hierarchies" (Kotliar and Wiens 1990) that characterize their response to environmental variation and influence their distribution and abundance patterns (Milne 1991). In their detailed study of the shrubsteppe bird community, Wiens and Rotenberry (see Wiens 1984) found very few patterns when they confined their analyses to shrubsteppe habitats alone. However, when they expanded the study to include several grassland habitats in addition to shrubsteppe, strong distributional patterns and habitat associations became evident. Similarly, if I were to expand the scale of my study to include other habitats, such as oak-pine, white pine, and red maple forests, I would expect Rufous-sided Towhees and Common Yellowthroats to begin to exhibit patchy dispersions and more well-defined habitat associations and to diverge from each other in these patterns as their full "ecological neighborhoods" were encompassed.

The results of my study suggest that the birds of the pine barrens were responding to factors such as habitat variation in an individualistic, scale-

dependent manner, pointing to the importance of looking at many scales in order to unravel the complex patterns of community structure (see also Rotenberry and Wiens 1991). Interspecific competition did not seem to be playing a role in influencing the distributional patterns and habitat associations detected. (In the beach analogy one would likely detect a strong negative correlation between birdwatchers and sunbathers, suggestive of competition.) One might expect Prairie Warblers and Common Yellowthroats to compete with one another simply because of their abundance and co-occurrence on all sites and their somewhat similar ecologies. However, because their territories heavily overlapped, it appeared that competition was not influencing their spatial distribution. But it might be influencing their foraging behavior.

Foraging Behavior. To gain a better idea of how Rufous-sided Towhees, Common Yellowthroats, and Prairie Warblers were using the habitat, I investigated foraging behavior, paying attention to intersexual as well as interspecific differences (Morimoto and Wasserman 1991b).

The analysis of 1624 foraging observations (900 Rufous-sided Towhee, 404 Common Yellowthroat, 320 Prairie Warbler) recorded in 1985 and 1986 revealed that differences in foraging height, plant species used as a substrate, position within a tree, and foraging maneuver were more pronounced between species than were male-female differences within species. This finding was not surprising for Rufous-sided Towhees, for which seventy-four to eighty percent of the foraging maneuvers recorded were on the ground. However, significant male-female differences did exist for Common Yellowthroats and Prairie Warblers. Furthermore the foraging behavior of female Prairie Warblers was more similar to that of Common Yellowthroats (especially males) than to that of male Prairie Warblers. What could explain such patterns?

The most straightforward explanation for these patterns is that the differences between male and female Prairie Warblers and Common Yellowthroats were due to sex-related constraints on their foraging behaviors (Holmes 1986), although the importance of male-female competition could not be entirely ruled out. Male Prairie Warblers often sang repeatedly from pitch pines, which served as scattered conspicuous song posts. Because of this behavior, these birds were likely to forage in these trees (forty percent of the observations were above three meters and in pitch pines compared with twenty-five percent for females). While male Common Yellowthroats were more opportunistic in their foraging height distribution, foraging at a variety of heights (depending on the availability of vegetation at those heights), they often sang from the tops of shrubs or from various heights in pitch pines, and thus their singing behavior may have been responsible for their foraging in these locations. The females of both species nest on or near the ground and thus, due to nest-related activities, forage closer to the ground. While male Rufous-sided Towhees often sang well above the ground, they were likely strongly influenced

by their need to scratch for food to forage primarily on the ground, resulting in no significant intersexual differences in this ground-nesting species. Once again, it was not necessary to invoke interspecific (or intersexual) competition to explain the patterns detected. Rather, sex-related and anatomical constraints were sufficient to explain the observed patterns. Finer-scale comparative studies of foraging behavior and reproductive success in overlapping and nonoverlapping territories, and in sites where only one species is abundant, are needed to address the question of interspecific competition more closely.

The results from these analyses adds more pieces to the complex puzzle of bird community structure. But many pieces remain. So far, I have looked at habitat associations, distributional patterns, and foraging behavior of individual species. Additional insight can be gained by investigating whole-community patterns (Maurer 1985). Such large-scale patterns raise questions about the effects of natural and human-caused disturbance on bird communities.

Whole-Community Patterns. The major community-level pattern emerging in this study was that plots burned most recently, with more open and patchy habitats, had the highest bird density and highest species richness (number). The message for conservation and management is clear: to preserve the most diverse and unique bird communities in the pine barrens (including the dense populations of Rufous-sided Towhees, Common Yellowthroats, and Prairie Warblers) open habitats must be maintained along with an array of more mature habitats, together comprising a rich patchwork mosaic. Prescribed burning seems to be the most appropriate way to maintain these open areas. Myles Standish State Forest is being considered for management under such a scheme with zones varying in the degree to which they restrict human activity. Other pine barrens sites, such as the pine barrens of Mashpee, would benefit from similar management schemes.

Today, a housing development sits on part of what used to be one of my favorite sites in Mashpee. While I might be saddened by this occurrence, it does provide an opportunity to evaluate the effects of habitat fragmentation on the pine barrens bird community (see Kerlinger and Doremus 1981). Fragmentation of open habitats may have different effects than fragmentation of forested habitats (Langen et al. 1991), about which much more is known (Saunders et al. 1991). Such information is needed if we are to be better equipped to approach the conservation and management of the pine barrens in a balanced way. From my own study it became clear that sites situated closer to housing developments and occurring on parcels of land that were more dissected by roads, had more birds which are traditionally associated with human habitations. We need to know what effects, if any, this has on the community in the long run. We also need to know how large a pine barrens site must be in order to maintain the bird community. Importantly, these questions must be addressed with a consideration of the landscape mosaic within which the pine barrens are embedded, with

attention to factors such as patch shape, number, and configuration, the presence or absence of vegetated corridors connecting patches, and the effects of the surrounding matrix (e.g., agricultural versus suburban). The conservation of the rich pine barrens ecosystem would allow the unique and interesting bird community to persist, and it would allow us to continue to explore and experience its wonderful complexity.

References

Addicott, J.F., J.M. Aho, M.F. Antolin, D.K. Padilla, J.S. Richardson, and D.A. Soluk. 1987. Ecological Neighborhoods: Scaling Environmental Patterns, *Oikos* 49: 340-346.

Holmes, R.T. 1986. Foraging Patterns of Forest Birds: Male-Female Differences, *Wilson Bulletin* 98: 196-213.

Kerlinger, P., and C. Doremus. 1981. Habitat Disturbance and the Decline of Dominant Avian Species in the Pine Barrens of the Northeastern United States, *American Birds* 35:16-20.

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: 253-160.

Langen, T.A., D. Bolgen, and T.J. Case. 1991. Predation on Artificial Bird Nests in Chaparral Fragments, *Oecologia* 86: 395-401.

Maurer, B.A. 1985. Avian Community Dynamics in Desert Grasslands: Observational Scale and Hierarchical Structure, *Ecological Monographs* 55: 295-312.

Milne, B.T. 1991. Heterogeneity as a Multiscale Characteristic of Landscapes, in *Ecological Heterogeneity* (J. Kolasa and S.T.A. Pickett, eds.), New York: Springer-Verlag.

Morimoto, D.C. 1992. Anything But Barren: The Search for Patterns in the Breeding Bird Community of the Massachusetts Pine Barrens, *Bird Observer* 20(2): 77-82.

Morimoto D.C., and F.E. Wasserman. 1991a. Dispersion Patterns and Habitat Associations of Rufous-sided Towhees, Common Yellowthroats, and Prairie Warblers in the Southeastern Massachusetts Pine Barrens, *Auk* 108: 264-276.

Morimoto, D.C., and F.E. Wasserman. 1991b. Intersexual and Interspecific Differences in the Foraging Behavior of Rufous-sided Towhees, Common Yellowthroats, and Prairie Warblers in the Pine Barrens of Southeastern Massachusetts, *Journal of Field Ornithology* 62: 436-449.

Rotenberry, J.T., and J.A. Wiens. 1991. Weather and Reproductive Variation in Shrubsteppe Sparrows: A Hierarchical Analysis, *Ecology* 72: 1323-1335.

Saunders, D.A., R.J. Hobbs, and C.R. Margules. 1991. Biological Consequences of Ecosystem Fragmentation: A Review, *Conservation Biology* 5:18-32.

Wiens, J.A. 1984. On Understanding a Nonequilibrial World: Myth and Reality in Community Patterns and Processes, in *Ecological Communities: Conceptual Issues and the Evidence* (D.R. Strong, Jr., D. Simberloff, L.G. Abele, and A.B. Thistle, eds.), Princeton: Princeton University Press.

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