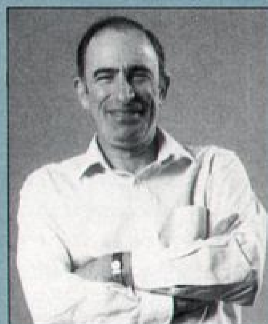
Paul R. Ehrlich

BIRDING FOR FUN



Birds, Butterflies, and Forest Patches

Illustration by Darryl Wheye

One of the most common words in the vocabulary of conservation biologists is a "patch." From their point of view, and that of most birds, the natural world is being reduced to a mosaic of habitat patches—islands in a sea of human disturbance. Very often, these are remnant patches of forest in a landscape of suburbs, farms, or pastures (or all three). As you may recall from a previous column (*American Birds*, Vol. 47, No. 3), Gretchen Daily and I discovered that whether or not an aspen patch in Colorado supported nesting Red-naped Sapsuckers (and the swallows dependent upon used sapsucker holes) depended upon the proximity of patches of willows to the aspens.

But general rules for what governs whether birds (or other organisms) can maintain themselves in a patch are still being worked out.

The best known theory on patch occupancy was developed in the 1960s by Robert MacArthur and E.O. Wilson. Robert MacArthur, a superb theoretician, was a dedicated birder whose doctoral dissertation was a seminal study of differences in how and where different species of warblers got their food. Ed Wilson, despite my attempts to convert him to butterflies or birds, remains the world's greatest authority on ants. He founded the science of sociobiology, and has just written an outstanding book on biodiversity and the extinction crisis, *The Diversity of Life* (which is a must for every reader of this column). Together MacArthur and Wilson hypothesized that the number of species found on an island would be determined by rates of species immigration and rates of species extinction. These rates would vary with island size (area) and distance from the mainland. The number of species would be essentially constant, but the exact mix of species would change because of "turnover"—new species arriving and old ones going extinct.

The equilibrium theory of island biogeography has done just what good theory is supposed to do. It has helped us to think about possible underlying regularities in an extremely complex world, and it has stimulated a great deal of research. Early on, the theory was generalized from simply dealing with oceanic islands to, among other things, dealing with islands of habitat—in other words, patches. It predicted, for example, that if a wooded landscape were cleared of all but scattered patches of trees, each of those patches would eventually hold fewer species than had the original forest. Thus, the diversity of the avifauna occupying each newly isolated patch would, over time, "relax" to a lower number of species. That number would be determined by the size of the patch and its distance from other patches and the remaining "mainland" (the nearest large tract of relatively undisturbed forest).

This column is no place to review the disputes that have centered around how well organisms (especially birds) in patches have conformed to the theory. My reading of the massive literature is that, while some studies show pretty convincing turnover, and signs of relaxation to lower levels of diversity in small patches are common, most "fits" of actual data to the theory are pretty poor. One reason is that island or patch size, as MacArthur and Wilson themselves realized, could very well be a surrogate for habitat heterogeneity. A large patch would, all else being equal, be more likely to contain a diversity of habitats than a small one. And, in general, more different habitats mean more species. So, in part, what may be needed is a theory to explain how immigration, habitat heterogeneity, and extinction interact.

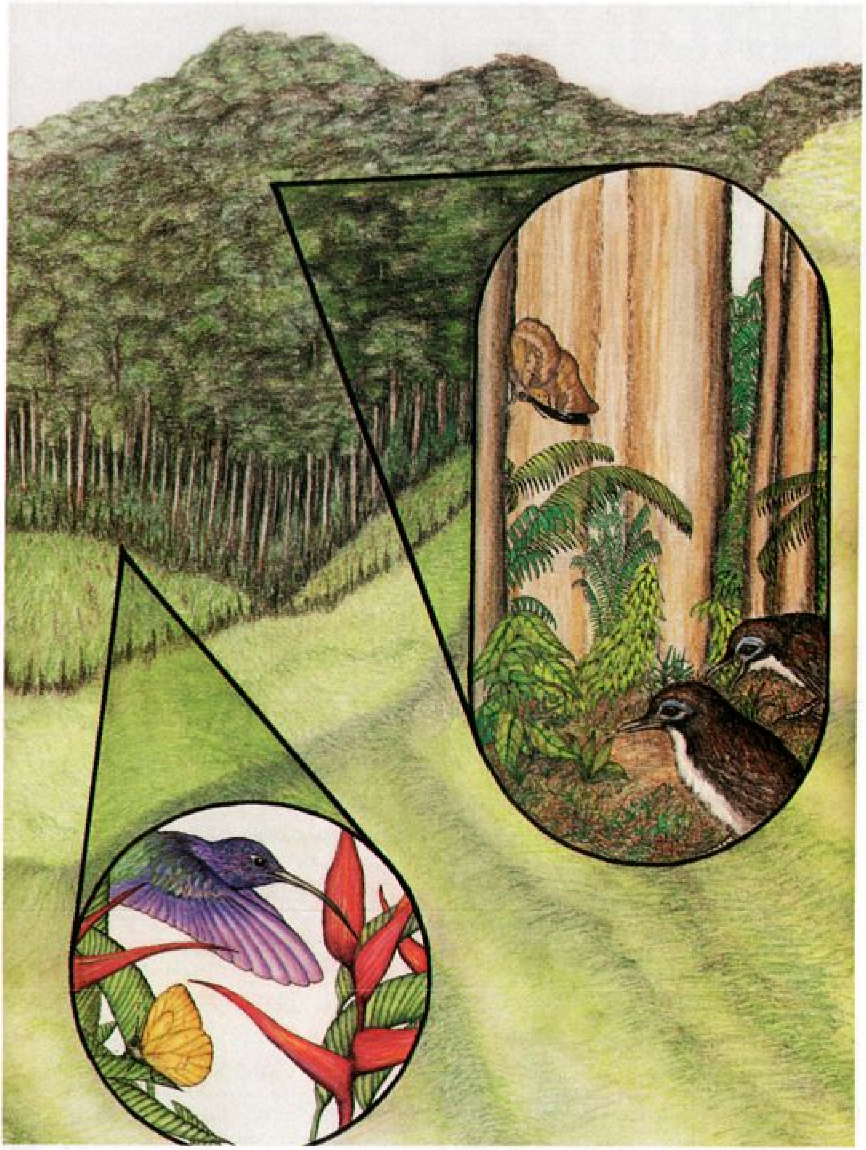
But the situation is not that simple. Unlike waifs blown out to sea that will try to colonize the first island they are fortunate enough to find, birds flying over a continental landscape apparently can choose among patches, finding one to their liking. In North America some migrants, especially those that winter in the tropics, prefer large tracts of forest for breeding. For certain species, such as the Ovenbird and Kentucky Warbler, breeding abundances seem to be very heavily influenced by the size and degree of isolation of patches. Others, often permanent residents or short-distance migrants, such as Gray Catbirds, Blue Jays, Carolina Chickadees, and Rufous-sided Towhees, do just fine in suburbs and may be found in very small patches or around the edges of large ones. Also, at least among birds that frequent aspen patches, there appears to be a tendency for many species (such as House Wrens and Warbling Vireos) to be found in virtually all patches above a certain critical size—that size differing from species to species and possibly from area to area.

There are other complications. Smaller patches inevitably differ from larger ones in more than size alone. They often will lack the area to maintain large predators such as wolves, grizzly bears, jaguars, or large forest raptors—yet the birds in them may be more vulnerable to extermination by human hunters. Changes in the abundance of these predators (what ecologist John Terborgh has called "the large things that run the world") can greatly modify food chains, leading to changes both in the size of populations of smaller animals and, in turn, in the composition of the plant community (which provides food for most birds).

In addition, there is the problem of "edge effects." While there may appear to be a sharp dividing line between a forest and an open field, for many organisms the division is much more complex. For example, light and wind from the open area penetrate into the forest, changing temperature and humidity and altering the conditions for plant growth, the abundances of insects and other small animals, the density of predators to which forest-dwellers are exposed, and so on. Based on the work of Tom Lovejoy and his collaborators in the Amazon, among others, and of my colleague Tom Sisk in Costa Rica, it appears that edge effects may penetrate up to a kilometer into rainforest.

Sisk has shown that in both the tropics and in the temperate zone, different bird species react differently to edge effects. Thus, while a Bicolored Antbird may suffer a reduction in population density in thick rainforest up to 250 meters from a "hard edge" where a pasture begins, Violet Sabrewing hummingbirds often show increased density at the same border. At a "soft edge" between undisturbed forest and a partially logged remnant forest, some species, including many migrant warblers, may pay little attention to the edge.

Similarly, some temperate zone species, like Chestnut-backed Chickadees, a common oak woodlands resident at Stanford's Jasper Ridge biological reserve, were scarcer within 100 meters of the interface between the woodland and chaparral. Others, such as



A charaxine butterfly *(Archaeoprepona demophoon)* and the Bicolored Antbird *(Gymnopithys leucaspis)* inhabit tropical moist forests and avoid forest edges, while a sulphur butterfly *(Phoebis argante)* and the Violet Sabrewing hummingbird *(Campylopterus hemileucurus)* frequent disturbed edge habitats.

Rufous-sided Towhees, were more abundant near the edge than in either pure woodland or pure chaparral. And some, such as the Orange-crowned Warbler, showed no reaction to the boundary. There, as in the rainforest, some species are edge avoiders, others are edge exploiters, while still others are edge neutral.

Another avian ecologist, David Wilcove, in a series of classical experiments in the eastern United States, demonstrated a dramatic edge effect. By placing artificial nests containing quail eggs at various distances from forest-field edges, he showed that nest predation in small forest fragments (with proportionally more edge) was much more common than in large tracts of continuous forest. The effect was especially pronounced for migrants that nested on *or* near the ground, such as Black-and-white Warblers and Ovenbirds. Forest borders have abundant nest predators, such as Brown-headed Cowbirds, Common Grackles, Blue Jays, and American Crows.

Gretchen Daily and I are now working on the biogeography of a series of rainforest patches near the Las Cruces forest preserve of the Wilson Botanical Garden in Costa Rica. We have already shown, by trapping forest interior butterflies, that patches of 8–75 acres have few species, while the nearby 600-acre forest supports a comparatively rich fauna. There was only a weak correlation between patch size and species diversity—the most striking result was the rapid drop-off in number of species outside the large forest tract.

We plan to expand this work to see whether birds show similar patterns. A study of birds in forest patches in the Usambara Mountains of Tanzania showed a clear positive relationship between patch size and species diversity, with generally scarce species and forest interior species tending to disappear as patch size shrank. Whether birds in Costa Rica mimic the more abrupt pattern characteristic of butterflies or the more gradual decline with size as seen in the Tanzanian study remains to be seen.

Some of our preliminary observations are interesting. Crested Guans use the small patches, even though they are large birds, heavily hunted and characteristic of extensive forest. We had expected them to be rather reluctant to cross open areas. Will antbirds—true denizens of shady forest, which seem even less likely than guans to cross extensive open areas—persist in the small patches? Answers to such questions will help us give advice to local conservationists about the size and connections of patches that will best preserve the area's remaining biodiversity.

Interestingly, the 600-acre Las Cruces forest shows only minor signs of faunal relaxation (species loss) after several decades of isolation. About 5 percent of previously recorded species have disappeared or greatly declined. On the other hand, one very early morning this April, I saw a Scaled Antpitta in the forest, an unrecorded species, and in August a Rufous-breasted Antthrush was seen, another new record for the forest. These, of course, were probably overlooked before, but they could also be immigrants. It will be interesting to see at what level the avian diversity of this large patch stabilizes—if it does.

It is clear that much more must be done to improve our understanding of how organisms react to increasing patchiness in their habitats. In particular, it is important to discover how much the reactions of well-known "indicator" organisms such as birds and butterflies also tell us about what is happening to less obvious but equally important organisms such as bats and beetles. Humanity is going to make the world increasingly patchy, and conservation biologists need to know which patches are most important to save.

—Paul R. Ehrlich is Bing Professor of Population Studies at Stanford University, and co-author of The Birder's Handbook, Birds in Jeopardy, *and* Healing the Planet.