THE DOUBLE EDGE EFFECT

by John C. Kricher

Ecologists and birders alike have long known about a phenomenon called "edge effect." If you want to see a high number of bird species, just patrol along an edge, where one kind of habitat gives way to another. A walk along a New England forest-field border will yield Brown Thrashers, Gray Catbirds, Rufous-sided Towhees, and Blue-winged Warblers along with brushy area species such as Field Sparrows and Common Yellowthroats and woodland species such as Ovenbirds, Scarlet Tanagers, and Northern Orioles. A few species, thrasher and towhees, for instance, are considered "edge specialists." Their highest abundances occur in such habitats. Moreover, many more species, each typically associated with either fields or forests, can nonetheless be encountered along an edge.

Edge effect is evident in the Neotropics as well. Forest borders are typically areas of bright sunlight, where many species of fruiting trees can be found as well as flowering vines and various epiphytes. Mixed species flocks of insectivorous birds such as greenlets and wood creepers, as well as fruit and nectar feeders including hummingbirds, tanagers, honeycreepers, and parrots, are characteristic of such areas. Edge specialists such as Great Antshrike and several saltator species skulk amid the dense junglelike vegetation of forest borders throughout Latin America.

Edge effect is currently increasing in both temperate and tropical latitudes. Any New England birder knows that throughout the region, from Connecticut to Vermont, forests and agricultural lands are being increasingly subdivided into house lots. Tracts of forest are being reduced to a scattering of "forest islands" dispersed within seas of housing developments and shopping malls. As forests become fragmented, edge increases. Likewise, in the tropics forests are being felled to create cattle pastures, plantations, and agricultural fields. Again, the result is a relative increase of forest edge and a decrease of forest interior. It is somewhat like cutting a block of ice into many small cubes. The net result is to greatly increase overall surface (edge) area relative to volume (interior forest). In the case of ice, the block melts sooner when subdivided. Though forests do not melt when cut into smaller fragments, the greater edge effect may exert a strong influence on bird species richness. The question is, is that influence for better or for worse?

Concern is becoming widespread over apparent recent declines among breeding populations of such species as Wood Thrush, Ovenbird, and Red-eyed Vireo. These species are long-distance migrants, each spending the winter months in some part or parts of the Neotropics. If their populations really are

shrinking—it is devilishly difficult to pin down meaningful population trends for widespread species—is the problem on the breeding grounds, on the wintering grounds, or during migration? At least in some areas, Brown Thrashers and Rufous-sided Towhees also appear to be in decline. These species are short-distance migrants, suggesting that at least part of the problem of declining species—even edge specialists—occurs on the breeding grounds. That problem may be too much edge effect and not enough interior forest. But how does this factor affect breeding success?

One species that is most definitely not in decline is the Brown-headed Cowbird. Christmas Bird Count data make it apparent that cowbirds have increased quite dramatically in the past thirty years (Brittingham and Temple 1983, Root 1988). Since cowbirds are brood parasites, females need to locate nests to parasitize. Cowbirds typically inhabit edge areas, steering clear of interior forest. As forests are fragmented, cowbirds become more successful because their victims are essentially brought closer to them by reductions in interior forest, normally areas of refuge from cowbirds. Recent studies of such species as Hooded Warbler, Worm-eating Warbler, and Wood Thrush (cited in Terborgh 1989) have all demonstrated alarming levels of cowbird parasitism. Possible declines in short-distance migrants such as towhees and thrashers might also be attributable, at least in part, to increased cowbird pressure, even though Brown Thrashers are capable of recognizing and rejecting cowbird eggs (Rothstein 1971, 1975). Many wood warbler species readily accept cowbird eggs.

Another species on the increase in the Northeast is the Blue Jay (Bock and Lepthien 1976). Blue Jays are efficient nest predators and thrive along woodland edges. If a Wood Thrush somehow manages to avoid becoming part of the "cowbird factory," its eggs or nestlings may still fall prey to marauding Blue Jays. Blue Jays are aided by bird feeders, which enable them to gorge on fat-rich sunflower seed and thus enhance their winter survival rate (Root 1988). Among the host of new books that have flooded the market about how to attract and feed wild birds, I have yet to see one point out that bird feeding, by reducing the natural mortality of Blue Jays, may contribute directly toward nest predation and hence, population decline of Wood Thrushes and their kindred.

Other nest predators such as American Crows, Common Grackles, and raccoons also thrive along edge areas and almost certainly add to reduced probability of nest success for a wide array of species. Recent research has strengthened the long held notion that nest predation is a highly significant factor in avian ecology (Ricklefs 1989).

In summary, forest fragmentation, by concentrating increasing numbers of birds nearer an edge, may be the cause of unnaturally high rates of brood failure among many species. Though cowbirds, Blue Jays, and raccoons may hold the

"smoking gun," we provided the ammunition—by shrinking the forests.

Now, what about the tropics? How does edge effect influence the ecology of migrants on their wintering grounds? One of the earliest generalizations about migrant passerines in the Neotropics was their apparent abundance in, if not outright preference for, forest borders and successional areas (Keast and Morton 1980, Rappole et al. 1983). Some researchers (Willis 1966, Leck 1972) suggested that the creation of disturbed habitats could augment survival on their wintering grounds for some species of migrants. In recent years that view has been increasingly challenged (Lynch 1989) as numerous censuses have revealed at least fifty-seven species of migrant landbirds that thrive in interior tropical moist forests (Wilcove and Terborgh 1984, Terborgh 1989). However, many, if not most, of these fifty-seven species are also found along edges and successional areas.

During January of 1982, 1983, and 1984 William E. (Ted) Davis and I, under grants from Earthwatch, studied migrant and resident bird distribution in three habitats in southern Belize. We compared the bird communities of an early old field, a young successional woodlot, and a mature moist forest. Both the early old field and woodlot were areas abandoned by the local Mopan Mayan farmers who practice slash-and-burn agriculture. They farm small plots, typically for as short as two to three years, and then abandon the plot, permitting it to undergo rapid ecological succession back to woodland.

I believe that slash-and-burn agriculture essentially mimics a pattern of natural disturbance that is normal for the American tropics (Kricher 1989). Wind-throw, mud slides, and other natural climate-induced disturbances have always been part of the tropics and thus have provided evolutionary selection pressures for uncounted generations of birds as well as other taxa. Mayan agricultural practices increase habitat patchiness, making the area a kind of ecological patchwork quilt of varying degrees of ecological succession. The Mayan farmers promote edge effect.

On our three study sites Ted and I identified 157 species, of which 31 were North American migrants. Interestingly, we sighted or netted slightly more species in each of the disturbed areas (102 and 98) than in the mature forest (87). Of the 157 species, 57 percent are described as forest border/edge species (Peterson and Chalif 1973, Ridgely 1976). The percentage of forest border/edge species was virtually the same in the three sites: 58, 56, and 57 percent. In total, only 42 species occurred on all three sites, and 65 species occurred on only one of the three sites. The distribution pattern between migrants and residents differed. The average migrant had a seventy percent chance of being encountered in more than one study site and thirty-two percent of the migrant species were found on all three sites. The average Neotropical resident species had but a fifty-five percent chance of occurring on more than one site. Thus

migrants, on the average, had a wider habitat distribution than residents. Our banding efforts indicated that migrants exhibited strong winter-site fidelity in both successional and interior forest areas (Kricher and Davis 1986).

Our study suggests that disturbed edge-type habitats in the tropics do, indeed, host an impressive diversity of resident species and form a major complex of habitats for North American migrants. Edge could well be essential for maintaining high species richness in the tropics. Why? Because edge has been created repeatedly and naturally through the millenia, and the birds have adapted to exploit it, just as have the sun-loving, rapid-growing plants that comprise it. Edges and successional areas may provide relatively rich sources of food for migrants. North American migrants do not nest in the tropics, so threats of nest parasitism and nestling predation along forest borders are not factors that influence migrants on their wintering grounds.

I am most emphatically not arguing that it is fine to cut large tracts of tropical forest. What the Mayans do is small-scale, temporary forest disturbance. Such a practice is in most cases profoundly different from large-scale, permanent habitat conversion that is occurring in many areas within the tropics, where forests are felled to create thousands of acres of pasture or cropland. Some migrant species such as the Cerulean Warbler, as well as numerous resident species, are utterly confined to forest interiors and stand to suffer potential reductions if forest acreage is lost. Because many forest species also utilize edge and successional areas, much of the species richness of disturbed areas and forest borders is utterly dependent on the immediate presence of accessible forest! What I am asserting is that within the normal ecology of the Neotropics, forest borders and edges do attract North American migrants, perhaps even disproportionately to other habitats, including forest interiors.

I sense an urgency among tropical researchers to justify forest preservation. I think this desire, however admirable, has led to a recent tendency to minimize the ecological importance of successional areas and edge, and, in some cases, to argue that even birds that occur in such areas would "prefer" to be in interior forest. I do not think the data, at least not our data, support such a notion.

At this particular juncture in evolutionary time, some North American migrants may suffer from edge effect on their northern breeding grounds but generally prosper from it on their tropical wintering grounds. Like the proverbial sword, the edge is double, and it seems to cut both ways.

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