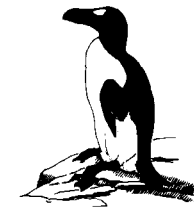
The Auk

A Quarterly Journal of Ornithology

Vol. 115 No. 1 January 1998



The Auk 115(1):1–3, 1998

OVERVIEWS

ANOTHER THREAT POSED BY FOREST FRAGMENTATION: REDUCED FOOD SUPPLY

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NEOTROPICAL MIGRATORY BIRDS and forest fragmentation will be forever linked in the literature. Scientists may debate about the extent to which migratory songbirds are declining, but few doubt that they are adversely affected by fragmentation. Severe negative demographic consequences of fragmentation have been documented at several spatial scales, including local (e.g. distance from edges), landscape (e.g. among tracts of different sizes and shapes), and regional (e.g. among landscapes that differ in forest cover). Yet, because of their huge global populations and high rates of natal and adult dispersal, Neotropical migrants keep recolonizing forest fragments in which their nesting success is extremely low. As a result, populations in fragmented forests can appear relatively stable even if their nesting success is far below levels necessary to compensate for adult mortality (i.e. they are population "sinks"; Brawn and Robinson 1996). For researchers, this provides an opportunity to study processes that would have caused local extinctions long ago in organisms that are less mobile than birds. For these reasons, Neotropical migrants have become flagship indicators of the negative consequences of fragmentation and of large-scale source/sink population dynamics.

Studies of one Neotropical migrant, the Ovenbird (*Seiurus aurocapillus*), have provided some of the best examples of extreme demographic problems caused by fragmentation. Ovenbirds are less abundant in small tracts and near edges, *and* most of the males in these areas are unmated. This startling result, first reported by Gibbs and Faaborg (1990), has been replicated several times (see Burke and Nol 1998, for a new replicate involving 69 forest fragments). Male Ovenbirds seem willing to waste their time defending territories near edges, but females avoid these areas.

Before reading Burke and Nol's paper, I had long assumed that Ovenbirds avoided small tracts and edges to escape from edge-preferring nest predators such as raccoons and snakes (Porneluzi et al. 1993). In Illinois, for example, the Ovenbird nests that we found in small tracts and near edges usually were destroyed by predators within a few days. Raccoons are so abundant in small Midwestern woodlots that it is hard to imagine any ground-nesting bird escaping them. Even along clearcut edges in New Hampshire, nest predation rates are higher than those in the forest interior (King et al. 1996). Avoidance of these predator-rich habitats by females clearly would be adaptive. Perhaps only surplus males sing near edges in an attempt to attract mates.

With the appearance of Burke and Nol's paper in this issue, however, the "predator-avoidance hypothesis" must be reevaluated. Burke and Nol provide the strongest evidence to date

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that arthropod abundance is reduced significantly along edges and in small woodlots compared with interior and larger sites. Many of us that study fragmentation effects have speculated about this possibility but were afraid to do the kinds of studies necessary to test it. Sampling insects is enormously labor-intensive, and the variances around mean estimates of insect abundance are so great (e.g. Holmes and Schultz 1988), that statistical inference is difficult (look at the error bars in figure 2 of Burke and Nol's paper for a prime example).

Undaunted by these logistical problems, Burke and Nol sampled arthropods from an impressive 17 woodlots. And, fortunately for them, the effects were large enough that their results were statistically significant. Female Ovenbirds clearly are very good at finding territories with rich food resources and avoiding areas in which food is scarce. As a number of foraging studies have shown, Ovenbirds are adept at finding and exploiting clumped prey, which appears to be the normal distribution of soil arthropods (Zach and Falls 1976). The same decision rules that cause foraging Ovenbirds to change directions more often after finding prey (Zach and Falls 1977) could apply to the larger question of choosing a territory. Territories with many rich food patches may trigger a response to settle and attempt to breed. Smith and Shugart (1987) provided support for this idea, showing that Ovenbird territories contain more food than nearby unoccupied sites, and that territory size is inversely correlated with food abundance. As Burke and Nol speculate, males may be more likely to choose territories based on conspicuous song perches, especially if they are unmated. Indeed, edges may provide the best opportunity for an unmated male to attract a dispersing female just entering a woodlot. For females, however, the drier, more desiccated leaf litter near edges may cause them to avoid these areas because of reduced food supply.

In this "food-based" hypothesis of habitat selection by female Ovenbirds, it may be a fortunate coincidence that edges and small forest tracts have both low food abundance and high rates of predation. Regardless of whether females choose territories based on perceived predation risk or food abundance, Ovenbirds avoid edges and small forest tracts, at least in the Ontario landscape studied by Burke and Nol. It is not difficult, however, to envision that in some landscapes, food resources may be more abundant in areas with high rates of predation. Foliage-dwelling arthropods, for example, may be more abundant near edges where foliage is particularly dense. In such a scenario, a food-based decision rule for selecting breeding sites could make birds susceptible to ecological traps (Gates and Gysel 1978). I suspect that the high densities of breeding birds in Illinois woodlots that almost certainly are population sinks (Brawn and Robinson 1996) may be a result of the rich soils of Illinois and excellent foraging conditions. The few nestlings in these woodlots that are not consumed by predators virtually never starve (pers. obs.). In this context, it would be very interesting to compare fledging rates at nests that escape predation in small versus large woodlots in Burke and Nol's study sites. These data would tell us a great deal about the extent to which food may be limiting to Ovenbird nesting success.

Thanks to Burke and Nol's study, we now have good evidence that fragmentation can reduce insect availability for some birds and indirect evidence of food-based habitat selection by females. Comparable studies of food-rich sites with high predation rates and vice versa would help disentangle the "predation-avoidance" and "food-based" models of nest-site selection. Some of us may dread the prospect of sifting through insect samples, but it looks as if the effort may be more likely to pay off than I would have expected.

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