Reproductive Performance of Territorial Ovenbirds Occupying Forest Fragments and a Contiguous Forest in Pennsylvania

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Introduction

Recent data (for example, Robbins et al. 1989*a*) have corroborated the occurrence of widespread population declines in several forest-interior songbirds that annu-

ally migrate to the neotropics. The Ovenbird (*Seiurus aurocapillus*), in particular, has registered declines in several populations (Askins et al. 1990; Hussell et al. 1992; and others).

Explanations for regional declines in avian populations include the fragmentation of forests in North America, where nesting occurs, and the clearing of tropical forests, where these birds reside during the nearctic winter (Askins et al. 1990). Forest fragmentation may

lead to higher rates of nest failure in forest-interior species because of increased predation (see Wilcove 1985; Yahner & Scott 1988) and nest parasitism (see Brittingham & Temple 1983) by Brown-Headed Cowbirds (*Molothrus ater*). Support for these notions, however, is mostly based on indirect evidence and small sample sizes (Robinson 1992).

Here, we report direct measures of reproductive success of individually-marked Ovenbirds nesting in a contiguous forest and adjacent forest fragments.

Methods

We established two study plots within a large, contiguous forest (more than 10,000 ha) in eastern Pennsylvania in 1988 and single study plots in 11 nearby forest fragments of various sizes (9.2–183.2 ha; Table 1) in 1990. Size of forests, percentage of forested land within a 2-km radius of the center of study plots, and core area (area of forest more than 100 m from edges; Temple 1986) were determined with a Numonics planimeter from aerial photographs taken in 1988. The forests of all study areas were dominated by oak (*Quercus* spp.), and their vegetation structure appeared to be similar.

We marked each study area in a rectangular x-y grid with flagged points spaced at 30.5 m.

Immediately after migrant Ovenbirds arrived (April 30, 1990), we attempted to capture all territorial males residing in study plots. We broadcast the Ovenbird vocalizations to lure birds into mist nets arranged around a model Ovenbird. Most birds were marked with a unique combination of color bands by May 18, and all but one bird were marked by the end of the breeding season.

Birds in the two large forest plots, River of Rocks and Owl's Head (Table 1), were individually marked and censused during three nesting seasons (1988–1990), and the study plots in nine forest fragments were censused in 1990. These 11 plots were censused at approximately four-day intervals throughout the breeding season (April 30–July 13). Two additional sites, the Dump and Shick plots, were only censused three and four times, respectively, because Ovenbirds did not establish territories at these sites (Table 1). Ovenbirds were present in all 13 forest plots during the migration period (April 30–May 15), and they had the opportunity to establish nesting territories. During morning censuses, locations of Ovenbirds detected were marked on grid maps, and band combinations and evidence of a mate, nest, or young were recorded. From mid-June to mid-July, we broadcast Ovenbird vocalizations during most censuses to aid in the location of marked males and their fledglings. No evidence of renesting by Ovenbirds was observed after the third week of July.

Males were classified as "paired" if they were seen interacting with a female, defending a nest or fledglings, or carrying food or nest material. Because nests of Ovenbirds are difficult to find, we classified males as successful if we observed them in the company of fledglings. We believe that this technique provides an accurate indication of whether a given male is successful or not. Fledglings frequently emit a weak "chip" call and remain with their parents until about 30 days of age (Hann 1937). To insure that all successful broods were detected, we censused all territorial birds frequently (about every four days) throughout the period when fledging occurs (mid-June to mid-July). With this method, we estimated a minimum success rate, as some males with fledglings may wander off study plots undetected. This bias plausibly occurred only on large-fragment (more than 70 ha) or large-forest plots, because birds caring for fledglings in small patches would be unlikely to lead offspring through nonforested (unsafe) habitat.

Table 1.   The estimated density of territorial male Ovenbirds and forest characteristics of study plots.

Site	Forest Area (ha)	Core Area (ha)	Study Plot Area (ha)	Distance to Large Forest (km)	Percentage of Forest within 2-km Radius	Plot Density of Ovenbirds (males/10 ha)
River of Rocks	>10,000	>10,000	19.5	0	97.2	6.6
Owl's Head	>10,000	>10,000	19.3	0	96.5	7.2
Gun Club	183.2	47.8	7.8	10.6	50.5	3.8
Snook	183.2	3.2	10.9	11.2	42.7	1.8
Spitzenburg	126.5	45.3	8.8	2.4	35.7	6.8
Laudadio	45.0	10.0	7.6	8.2	29.0	1.3
Dixon	44.7	2.3	16.4	7.0	22.9	1.8
Deturk	41.9	0.2	28.8	6.1	18.0	0
Kunkle	23.4	2.5	23.4	9.1	20.9	0
Kehl	19.4	<0.1	7.8	3.3	27.4	2.6
Lilienthal	18.7	1.4	18.7	11.8	42.7	0
Shick	13.7	0.3	13.7	10.9	12.2	0
Dump	9.2	0.2	9.2	6.7	23.4	0

Results

Of the 13 study plots, 8 contained territorial Ovenbirds (Table 1). Density of resident males was positively related to the percentage area of forest within 2 km of study plots ($F = 18.2, R^2 = 0.623, p < 0.001$), size of the forest ($F = 11.6, R^2 = 0.514, p = 0.006$), and core area ($F = 11.3, R^2 = 0.508, p = 0.006$), and negatively related to the distance of a large forest ($F = 15.0, R^2 = 0.577, p = 0.003$). The linear relationship between all four forest variables, in combination, to bird density produced a R^2 of 0.842 ($F = 16.0, p < 0.001$). The two-variable model that best explained Ovenbird density included percentage area of forest and distance to a large forest ($F = 15.6, R^2 = 0.758, p < 0.001$).

The proportion of male Ovenbirds classified as paired was greater in the large-forest plots ($67\%, n = 27$) than in fragments ($47\%, n = 17$), but the difference was not significant ($G = 1.59, p > 0.1$).

The proportion of successful males (seen with fledglings) did not differ ($G = 0.05, p > 0.5$) between the two contiguous forest plots in 1990 (57% & $62\%, n = 14$ & 13, respectively). Also, the success of Ovenbirds did not change ($G = 0.44, p > 0.5$) on the large forest plots between 1988 and 1990 ($58\%, n = 31; 50\%, n = 20; 59\%, n = 27$; respectively).

Assuming that Ovenbirds had the potential to breed in all study areas, the 11 plots sampled intensively provided the most appropriate experimental units for statistical analysis (Hurlbert 1984). This analysis revealed that large-forest plots contained significantly (Wilcoxon test, $z = 2.56, p = 0.01$) more successful males (median = 8, $n = 2$) than the forest fragments (median = 0, $n = 9$). Analysis including only sites where Ovenbirds became established ($n = 8$; Table 1), also indicated a significant difference between large forests and fragments ($z = 2.12, p = 0.03$).

Perhaps biologically more meaningful, the difference in the proportion of successful males between the large forest plots ($59\%, n = 27$ males) and the forest fragments ($5.9\%, n = 17$ males) was dramatic (Fig. 1). Statistical comparison of these values suggests a highly significant difference ($G = 14.0, p < 0.001$). Only one male Ovenbird in the fragments sampled was successful, and he resided in one of the largest fragments (126.5 ha); five other territorial males in the same fragment failed to produce fledglings.

Five nests were located on the large-forest plots and three within forest fragments. Two of the nests within small forests ($67\%; n = 3$) were destroyed by unidentified predators; a single cowbird and Ovenbird successfully fledged from the third nest. No cowbird eggs were observed in nests found in the large forests, but one marked Ovenbird occupying a large-forest plot was seen feeding a cowbird fledgling.
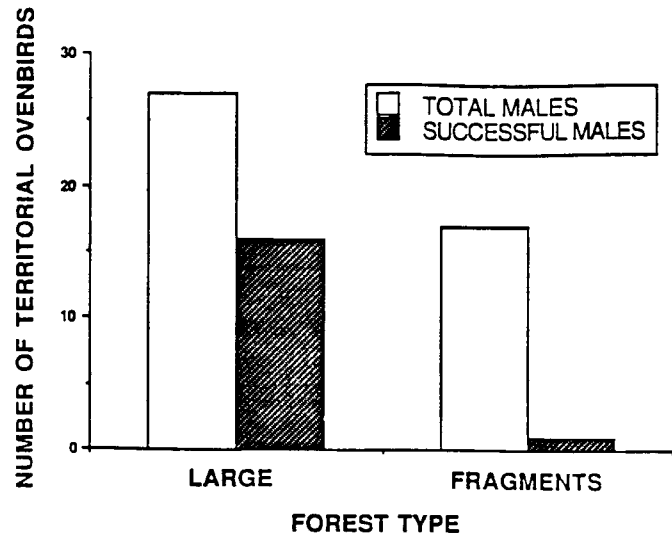

Figure 1. The numbers of observed and successfully reproducing territorial male Ovenbirds occupying large- and fragmented-forest study plots in eastern Pennsylvania.

Discussion

Although reproductive dysfunction has been suggested to occur in fragmented forests (Temple & Cary 1988; Askins et al. 1990; Blake 1991), it has been inferred from limited evidence or from presence-absence data (Robinson 1992). Our data show that at least 1.19 young/male Ovenbirds were produced in the large forest ($n = 27$ males), whereas only 0.06 young/male ($n = 17$ males) were fledged on fragments, a 20-fold difference. This difference in nesting success between large and small forests was greater than the four-fold difference reported previously (Temple & Cary 1988).

One limitation of our results is that the dramatic pattern observed was based on one year of data. Our comparison using the number of plots sampled ($n = 11$) as the experimental unit for analysis, however, suggests that a significant difference occurred in 1990 ($p = 0.01$) and may be inferred to the larger landscape. Even if the significant depression observed in reproductive success occurs only infrequently, this pattern would place Ovenbirds nesting in fragments at a tangible disadvantage. Because much of the forest in Pennsylvania and elsewhere is configured into relatively small fragments (Brooks 1989), the documented reproductive dysfunction in these habitats could account for the reported decline in Ovenbirds (Hussell et al. 1992 and others).

Our data support the existence of a source-sink Ovenbird population, in which large forests represent sources of production and excess reproductively-mature birds occupy sinks within forest fragments (Pulliam 1988). Sink populations are maintained pre-

sumably by the "rescue effect"—the continuous influx of Ovenbirds produced in the source habitats (Brown & Kodric-Brown 1977).

Three of the forest fragments sampled were relatively large (more than 100 ha) and contained numerous singing Ovenbirds. Plot density of males (6.8/10 ha) within one of the larger fragments was equivalent to estimates determined for large-forest plots (Table 1). The fragment, Spitzenburg, accommodated a high density of Ovenbirds, but it did not support a reproductively successful population. This finding illustrates the danger of using presence-absence data to infer the size of habitat patches needed to support functioning populations of songbirds (see Robbins et al. 1989b; Blake 1991). Within eastern Pennsylvania, our data suggest that forests as large as 183 ha do not sustain functional breeding populations of Ovenbirds.

The mechanism depressing reproductive success within fragments was not determined. A lower proportion of males were seen consorting with females in the fragments than in the large forest, but this difference was not significant. If paired males in fragments experienced reproductive success rates similar to those in the large forest, at least five male Ovenbirds using small forests should have reared fledglings; we observed only one successful male. A lack of available females may contribute to lower reproductive success within fragments (Gibbs & Faaborg 1990), but this does not completely explain the poor fledgling production by Ovenbirds in forest fragments in Pennsylvania.

Contrary to findings elsewhere (Brittingham & Temple 1983; Robinson 1992), cowbird parasitism does not seem to affect Ovenbirds seriously in either fragments or large forests in Pennsylvania. In fragments, one cowbird egg was found in the three nests located, and no adult Ovenbirds ($n = 17$) were seen feeding cowbird fledglings. In the large forest, no cowbird eggs were present in the five nests we located, and only one of 33 fledglings being cared for by marked Ovenbirds was a cowbird.

Alternatively, we suspect that predation (Wilcove 1985; Robinson 1992) may be a prominent factor affecting reproductive performance of Ovenbirds exploiting fragments (two of three nests monitored were depredated). Other phenomena may also contribute to reproductive dysfunction in small forests, however, such as increased interspecific competition with "edge" species (Ambuel & Temple 1983), changes of habitat structure caused by the presence of edge plants, and variation in microclimate.

Although forest cover within eastern North America is no longer decreasing, the available forest continues to be fragmented (Brooks 1989). On the basis of our data, we suggest that if the area of forest habitat remains unchanged, but the ratio of small forest fragments increases relative to large forests, Ovenbird populations

could undergo severe decay. If the process of forest fragmentation continues on a continental scale, profound reductions in the forest-interior avifauna populations of North America may occur.

Acknowledgments

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