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LANDSCAPE AND FRAGMENT SIZE EFFECTS ON REPRODUCTIVE SUCCESS OF FOREST-BREEDING BIRDS IN ONTARIO

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Abstract. To determine the minimum size requirements and influence of landscape context on reproductive success of forest-breeding songbirds, we monitored nesting success of five species of songbirds on 40 fragments (12–2350 ha in total woodlot size) and two continuous forest sites in south-central Ontario from 1994 through 1997. Woodlot size was the most important variable contributing to differences in reproductive success, with local forest cover (within a 10-km radius) having no significant additional effect on productivity for any species. For all species, except Red-eyed Vireo (*Vireo olivaceous*), adult female reproductive success was at or above replacement levels in large fragments (mean of 121 ha core area, 849 ha woodlot area) and continuous forest, and below replacement levels in small fragments (mean of 7.8 ha core area, 93 ha woodlot area). Red-eyed Vireo productivity was particularly low, with single-brooded females unable to maintain populations in any woodlots monitored, although populations were close to replacement levels in continuous forest. Only the very largest fragments acted as sources for Ovenbird (*Seiurus aurocapillus*) and Wood Thrush (*Hylocichla mustelina*) (i.e., >23 ha in core area, 225 ha in total woodlot area). Ovenbird and Wood Thrush were the most area-sensitive, and Rose-breasted Grosbeak (*Pheucticus ludovicianus*) and Veery (*Catharus fuscens*) the least, although all four species had significantly lower reproductive success in small as compared to large forest fragments. Reproductive success of Rose-breasted Grosbeaks and Veery were similar in large forest fragments and continuous forest and were close to maintenance levels in small fragments, despite published reports of significant declines that might be attributable to poor productivity. Nest predation was the major cause of nest failure, with brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) further reducing the number of host young fledged from Ovenbird and Red-eyed Vireo nests. Parasitism rates on the remaining species were very low and not analyzed statistically. Local forest cover had little effect on predation rate or rate of parasitism by Brown-headed Cowbirds. Although local forest cover had little effect on reproductive success within fragmented landscapes, nest success was significantly higher in continuous forest than in all fragments combined for both Ovenbird and Red-eyed Vireo. Our data show a poor agreement with Breeding Bird Survey population trend estimates for Ontario between 1986 and 1996. As only 1% of the forest fragments locally available are large enough to function as source habitats, we strongly advocate their preservation. We recommend preservation of forest tracts at least 500 ha in size, particularly woodlots with >90 ha in core area, to function as sources that will help guard against population declines on a local scale.

Key words: area effects; forest birds; forest fragmentation; landscape effects; Ontario, Canada; Ovenbird; Red-eyed Vireo; reproductive success; Rose-breasted Grosbeak; Veery; Wood Thrush.

INTRODUCTION

In the past decade, neotropical migrant birds nesting in deciduous forests of eastern North America have been reported to decline (Robbins et al. 1989, Askins et al. 1990, Sauer et al. 1996). A reduction in fecundity due to habitat fragmentation on breeding grounds appears to be a major contributing cause of observed population declines (Bohning-Gaese et al. 1993, Donovan et al. 1995, Robinson et al. 1995). Lower fecundity in fragmented forests occurs as a result of a reduction in pairing success (Gibbs and Faaborg 1990, Villard et al. 1993, Van Horn et al. 1995, Burke and Nol 1998), higher rates of nest predation (Wilcove 1985, Donovan et al. 1995, Hoover et al. 1995), and increased brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Donovan et al. 1995, Robinson et al. 1995). Those factors may act in concert to limit reproductive success of forest-nesting bird species through a reduction in recruitment of individuals into breeding populations (Donovan et al. 1995).

Landscape level processes appear to influence some factors related to avian nest success (e.g., parasitism; Hahn and Hatfield 1995, Robinson et al. 1995, Don-

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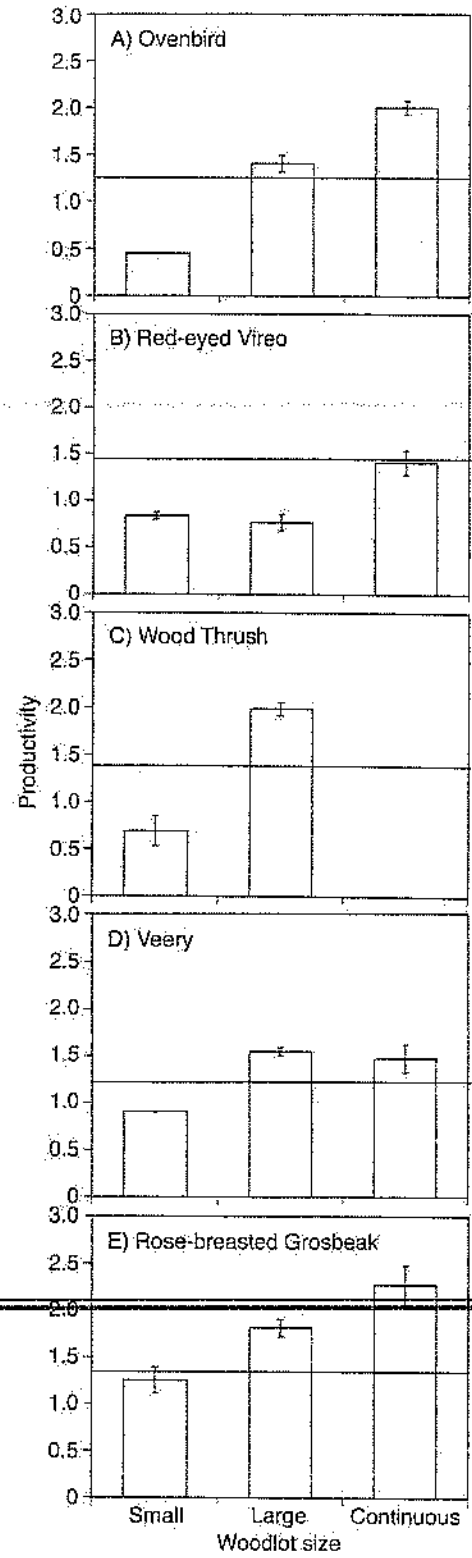

FIG. 4. Comparison of nesting success on small fragments, large fragments, and continuous forest for five species of forest-breeding songbirds in south-central Ontario, Canada. Data were collected from 40 forest fragments and two continuous forest sites between 1994 and 1997. Small fragments were <23 ha in core area, while large fragments were >30 ha in core area. The dashed line represents the threshold for source–sink habitat designation. Below this line, productivity does not compensate for mortality, and populations are sinks. Data are means ± 1 SE.

fy females were required to maintain populations. Under that scenario, populations on fragments were sinks, whereas populations in continuous forests seemed to be close to self-sustaining (Fig. 4B). Even if Red-eyed Vireo nesting in fragments double brooded, their populations would still be unable to balance adult mortality (Table 5). However, in continuous forest renesting would allow populations to function as sources, producing 1.7 fy female per adult female. As vireos produce only 0.36 fledged young females per nesting attempt on small fragments and 0.32 fledged young females per nesting attempt on large fragments, they would be required to nest 4–4.5 times in one season in fragmented landscapes to maintain populations.

Wood Thrush.—With a mean survival rate of 0.67 for adults, adult female Wood Thrush were required to produce 1.42 fledgling females to balance adult mortality. Wood Thrush in small fragments were population sinks while large fragments functioned as population sources (Fig. 4C). If Wood Thrush were able to nest three times in one breeding season, populations in small fragments could balance losses due to adult mortality (Table 5).

Veery.—With a mean adult survival rate of 0.623, adult female Veery needed to produce 1.2 fledged young females per year to maintain populations at their current levels. In our study, small fragments were populations sinks for nesting Veery, whereas populations in continuous forest and large fragments were weak sources (Fig. 4D).

Rose-breasted Grosbeak.—With a mean survival rate of adult grosbeaks of 0.57, 1.38 fy females would be required to balance adult mortality. In large fragments and continuous forest populations of double-brooded grosbeaks were above maintenance levels, while those in small fragments were sinks (but close to maintenance levels) (Fig. 4E). If local populations of Rose-breasted Grosbeaks do not double brood, large fragments would function as population sinks and continuous forest would be close to maintenance levels (Table 5).

DISCUSSION

For all species, the general trend in our study area was for nest success and number of young fledged from successful nests to be highest in continuous forest, and, within fragmented habitats, for large fragments to be more successful than small fragments. Populations of all bird species breeding in small forest fragments were habitat sinks, and without constant immigration of individuals from nearby source habitats, those populations would go extinct locally. The amount of local forest cover, which ranged from 13 to 54% within 10 km of the fragments, contributed little to the fragmentation effect observed for any species.

In this study, nest parasitism accounted for few total nest losses, but Brown-headed Cowbirds did significantly reduce mean number of host young fledged from Ovenbird and Red-eyed Vireo nests (i.e., parasitized nests had half as many fy Ovenbirds, and only 60% as many fy Red-eyed Vireos as nonparasitized nests). Parasitism rates reached 24–30% in small fragments, yet vireos and Ovenbirds were able to fledge at least one young from 60% and 67% of all the nests parasitized, respectively. The effect of cowbird parasitism may be sufficient to prevent songbird populations from reaching replacement rates, in combination with high predation rates (Brittingham and Temple 1983) as is typical of fragmented landscapes. However, our data demonstrate that in south–central Ontario, parasitism by Brown-headed Cowbirds has not seriously reduced the ability of host species to fledge at least one young.

Nest predation accounted for the majority of total nest failures for all species in this study. As nest predation is typically the most important cause of nest failure (Martin 1992), preservation of forest interior birds will hinge on identifying factors that influence nest predation (Paton 1994, Donovan et al. 1997). Elevated nest predation rates characteristic of small fragments (Wilcove 1985, Small and Hunter 1988) hold many populations of forest birds well below replacement levels (i.e., sinks); this is particularly evident in our study area with Ovenbirds. Although we found no significant differences in predation rates with respect to local forest cover, in other geographic locations where local factors differ (i.e., differences in the predator community and/or abundance), those landscape effects may be important (as in Robinson et al. 1995, Donovan et al. 1997). It is also feasible that other features on a landscape scale besides local forest cover are having a significant effect on predation rates (e.g., proportion of wetlands, types of agricultural uses).

Some research suggests that predation pressure declines dramatically at distances beyond 45 m from the forest edge (Gates and Gysel 1978, Burger 1988, Paton 1994), although other studies suggest that predation pressure may extend 200–300 m into the forest interior (Wilcove 1985, Andren and Anglestam 1988) or show no edge effect (Mankin and Warner 1992, Rudnicky and Hunter 1993). The magnitude of that edge effect will depend on landscape composition as well as composition of the predator community, which may vary with woodlot size and with region (Nour et al. 1993, Haskell 1995). In our study, vulnerability of nests to predation was influenced by distance from nests to forest edge only for Veery and Rose-breasted Grosbeak nests, both suggesting a 100 m edge zone, with the most dramatic edge effects within the first 50 m. Additional evidence collected from sand traps supports a lack of edge effects on mammalian predator activity (D. M. Burke, *unpublished data*). Evidence against an edge effect on nest predation has been attributed to a lack of nest depredation by avian predators, which are commonly found near edges (Whitcomb et al. 1981, Donovan et al. 1997). Mammalian predators may be more abundant in small woodlots (Wilcove 1985) or highly fragmented landscapes (Donovan et al. 1997), suggesting that all nests in small fragments and/or agriculture-dominated landscapes would be vulnerable to depredation, not just those nesting near edge. Predation and parasitism rates may also be associated with edges only in predominantly agricultural landscapes or moderately fragmented landscapes (Martin 1992, Hahn and Hatfield 1995, Donovan et al. 1997). A ubiquitous edge effect on predation was not found in this study. However, higher brood parasitism rates occurred within 100 m of the forest edge. Cowbirds are typically identified as edge species, though that edge effect on parasitism rates is not universal (see Hahn and Hatfield 1995, Donovan et al. 1997).

Fragmentation can increase woodlot isolation, which may reduce immigration rates. In small fragments, immigration may be critical to population persistence, with source habitats supplying a pool of immigrants to sink habitats, with the effect of preventing local extinction. As populations of the target species remained relatively constant between 1994 and 1997 on the woodlots surveyed, despite poor reproductive success, a source–sink metapopulation would be suggested. Brawn and Robinson (1996) concluded from their study on reproductive success of migrants in Illinois that local population dynamics and local productivity were uncoupled, as species which were producing virtually no young maintained their populations through source–sink population dynamics. Immigration from source areas can sustain populations in patches where species would otherwise become locally, and permanently, extirpated, thereby preventing populations from registering significant declines in areas where productivity is nominal. Fragmentation in this study has probably not proceeded to the extent that woodlots under investigation are too isolated on a landscape scale to prevent immigration of colonists from adjacent source populations. Critical data on dispersal distances of juveniles from natal to breeding sites are lacking, and therefore we do not know the scale at which source–sink dynamics operate. Juvenile songbirds are thought to travel hundreds of kilometers between natal and breeding sites, which would mean that for most populations studied here, the continuous forest to the north would continue to act as a population source, even if large fragments which currently acted as sources were removed.

The underlying causes of the fragmentation effect and the sensitivity of different nesting and foraging guilds remain unclear. Ovenbirds nesting in small fragments in our study had the lowest reproductive success of all species, suffered highest rates of brood parasitism and high rates of nest predation (as in Robinson et al. 1995), and produced fewer fledglings from otherwise successful nests in small as compared to large fragments. This latter result appears to confirm that food is probably limiting in small fragments, both to attract females to those fragments (Burke and Nol 1998) but also to provide food for nestlings. Ground nesting species are frequently cited as the most vulnerable to predation (Wilcove 1985, Martin 1988, Bollinger and Linder 1994, but see Donovan et al. 1995, Martin 1995), have lower reproductive success (Bollinger and Linder 1994, but see Martin 1995), and are the first to disappear from small tracts of forest (Diamond 1976). Previous research also suggests that low nests are more vulnerable to cowbirds (Bohning-Gaese et al. 1993) and high predation rates on ground nests may reflect an increased abundance of raccoons and avian predators in fragmented landscapes (Hoover and Brittingham 1993).

Species with shrub nests in this study were less vulnerable to predation only in large fragments, for in small fragments ground and shrub nests were depredated at equal rates. That suggests that terrestrial mammals were the main predators impacting population trends in large fragments and that possible differences in predator communities within small and large fragments exist (Bohning-Gaese et al. 1993). However, Red-eyed Vireo nests were heavily depredated in all habitats, with Blue Jays (*Cyanitta cristata*) suspected as their main predator, for we witnessed many instances of adult vireos mobbing Blue Jays which were moving quietly through the trees, apparently looking for nests. This high rate of nest predation on shrub nests has been suggested elsewhere (Martin 1995). Further research might question the extent to which Blue Jays are willing to penetrate large fragments and focus on how densities of this common, but poorly studied species are affected by changes in fragment size and landscape.

We did not find a strong agreement between area-sensitivity on the breeding grounds (in terms of nest success) and the magnitude of population declines suggested by the BBS data from Ontario (Sauer et al. 1996). For example, in this study Rose-breasted Grosbeaks were the most successful, though small fragments still functioned as habitat sinks. The BBS data suggest that Rose-breasted Grosbeaks are experiencing one of the most significant declines of the five species that we studied (Sauer et al. 1996). It is possible that the general availability of suitable breeding habitat for grosbeaks has declined over the last 10 yr. Though populations may be sources in many habitats in which they occur, there may have been a general decline in density of individuals that remnant habitats can support (e.g., maturation of forests which may reduce nesting opportunities for grosbeaks). If Rose-breasted Grosbeaks are not area sensitive, and do not preferentially seek out breeding territories in large woodlots, a large proportion of their population may reside in sink habitats which are incapable of sustaining populations at current levels. As such, species which are less area-sensitive may be more vulnerable to population declines if a larger proportion of the breeding population occurs in sinks where reproductive dysfunction is high.

Our results on reproductive success of Red-eyed Vireos are somewhat puzzling. This species did not reach replacement levels even in continuous forests, but population trend data from both the BBS and migration counts indicate stable or increasing populations. As this species also nests in suburban habitats, its flexibility in habitat selection suggests that they may not be limited by amount of relatively intact forested habitat in southern Ontario.

As only 1% of the forest fragments locally available to forest-breeding songbirds are sources (>200 ha), and 82% have no core area, the majority of patches available are habitat sinks. The few source habitats available occupy <30% of the total forest cover still present in this region of south-central Ontario, and further loss of those habitats is likely to jeopardize local songbird populations. Those large forest patches may contain the majority of local populations of some songbirds (e.g., species like the Ovenbird which select larger fragments and show area-related changes in density and pairing success, Burke and Nol 1998). Loss of these habitats would probably result in dramatic local population declines.

For some species destruction of wintering habitat may contribute more significantly to the observed declines, particularly for species whose fecundity levels are at or close to maintenance levels. Veery and Ovenbird populations are predicted to decline due to habitat loss on the wintering ground (Rappole 1995), and that loss of wintering habitat may be more significant for those species, even though fragmentation on the breeding grounds may exacerbate the situation. Hence for Veery, despite moderate reproductive success in fragments, population declines may be due to wintering ground phenomenon. Our data indicate that, for Ovenbird, reproductive success is not correlated with densities obtained using point count censuses such as those used to obtain BBS data. However, reproductive success is strongly correlated with pairing success and moderately correlated with spot-mapping densities (Burke 1998). As such, point-count estimates may offer little insight into the value of a particular habitat for breeding productivity. Other species may, however, show stronger correlations between reproductive success and point-count estimates, particularly if those species do not show area-related changes in pairing success. More data are needed to determine how pairing success changes with area for the other species investigated. Trend data from migration stopover sites may more closely match trends predicted based on results of this study than BBS data. For Wood Thrush, a species that is very scarce in the continuous forest to the north of our study site, and therefore relies solely on fragments for reproduction in our area as a source of breeding birds, trend estimates based on point-count censuses and migration data may show stronger correlation with data obtained by monitoring regional reproductive success. This is expected to occur when all regional populations are sinks.

Our results provide additional support for the conservation of forest nesting migrant songbirds by identifying, preserving, and restoring large tracts of forest which will function as population sources and safeguard against the collapse of some local populations. This is not to say that sink habitats are without value. Most fragments with nesting Ovenbirds produced at least one fledgling over the course of the study, and some of those fragments may occasionally function as source populations. Sink populations can have a positive influence on metapopulation size and longevity, providing source populations remain (Howe et al. 1991, Davis and Howe 1992, Donovan et al. 1995). Data collected on nest success of area-sensitive species such as the Ovenbird indicate that forests <500 ha in total size (90 ha in core area) will represent habitat sinks. Although loss of sink habitats may contribute to overall population declines, conservation efforts should be directed towards identification and protection of large forest fragments in otherwise settled landscapes.

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