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Effects of Exotic *Lonicera* and *Rhamnus* on Songbird Nest Predation

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Abstract: *Habitat fragmentation and disturbance exacerbate the invasion of exotic plant species that, in turn, may attract nesting songbirds by providing a branch structure suitable for nest sites. We document that American Robin (Turdus migratorius) nests in two exotic plants, Lonicera maackii and Rhamnus cathartica, experienced higher predation than nests built in comparable native shrubs (Crataegus, Viburnum) and native tree species. This was due to a combination of lower nest height, the absence of sharp thorns on the exotic species, and perhaps a branch architecture that facilitated predator movement among the exotic species. In a more subtle interaction, nesting Wood Thrushes (Hylocichla mustelina) experienced apparent competition with robins for nest sites in Lonicera, and this interaction was further aggravated by an increased selectivity for Lonicera by nesting robins, possibly due to their early leaf flush and expansion. By documenting increased nest predation in songbirds nesting in exotic shrubs, our results suggest that restoring native plant communities may benefit the surrounding avian community.*

Efectos de las Especies Exóticas *Lonicera* y *Rhamnus* en la Depredación de Nidos de Aves Cantoras

Resumen: *La fragmentación y perturbación de hábitats incrementan la invasión de especies de plantas exóticas que, en turno, pueden atraer aves cantoras anidando al nidos del zorzal americano (Turdus migratorius) en dos plantas exóticas, Lonicera maackii y Rhamnus cathartica, que experimentaron mayor depredación que los zorzales que construyeron nidos en arbustos nativos comparables (Crataegus, Viburnum) y en especies nativas de árboles. Esto se debió a la combinación de una altura del nido mas baja, la ausencia de espinas filosas en las especies exóticas y probablemente a una arquitectura de ramas que facilitó el movimiento de depredadores entre las especies exóticas. En una interacción mas sutil, el zorzalito maculado (Hylocichla mustelina) experimentó una aparente competencia con el zorzal americano por sitios de nidación en Lonicera, esta interacción fue agravada aún mas por una creciente selectividad por Lonicera por zorzal americano, posiblemente debido a sue temprano desarrollo de hojas y expansión. Al documentar el incremento en la depredación de nidos en aves cantoras anidando en arbustos exóticos, nuestros resultados sugieren que la restauración de comunidades de plantas nativas podría beneficiar las comunidades de aves de los alrededores.*

Introduction

Exotic plant species in the genera *Lonicera* and *Rhamnus* have invaded numerous sites throughout much of temperate, eastern North America. *Lonicera maackii*, for instance, is now widespread in at least 25 states east

of the Rocky Mountains (Luken & Thieret 1996; Hutchinson & Vankat 1997). Where they occur, *Lonicera* and *Rhamnus* provide a branch structure suitable for nest construction within the range of heights used by many songbird species (Whelan & Dilger 1992, 1995). These shrubs therefore may act as ecological traps if songbirds nesting in them experience higher predation than comparable native shrubs (Gates & Gysel 1978).

Habitat fragmentation exacerbates both the invasion of exotic plant species (Hobbs & Huenneke 1992; Hutchinson & Vankat 1997) and higher nest predation

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(e.g., Robinson et al. 1995), but to the best of our knowledge these two processes have never been causally linked. If nest predation is higher in exotic species, this may provide one potential mechanism for the population declines seen in some songbird species occupying this region. For instance, both Mills et al. (1989) and Germaine et al. (1998) found that native bird species diversity and density were positively correlated with the volume of native vegetation but were negatively correlated or uncorrelated with the volume of exotic vegetation. The link between invasion of exotic shrubs and population declines, if it exists, will take much research to uncover. We examined the connection between exotic species and nest predation rates.

We document nest predation on two songbird species, American Robins (*Turdus migratorius*) and Wood Thrushes (*Hylocichla mustelina*), over 6 years in an urban reserve outside of Chicago. Both *Lonicera* and *Rhamnus* (predominantly *R. cathartica*) are abundant at the site where they have replaced native species of *Viburnum* and *Crataegus*. *Rhamnus* lack the sharp thorns that characterize *Crataegus*, whereas *Lonicera* has sturdy branches and reduced basal cover relative to *Viburnum* (K.A.S., personal observations). We hypothesize that these features may increase nest predation directly through predator facilitation. Furthermore, early leaf flush and expansion in *Lonicera maackii* (Trisel & Gorchov 1994) may make them a focus for nest building. Concentrating nest densities by nesting in a restricted subset of plant types available may in turn attract generalist predators to these aggregations of nests (Martin & Roper 1988; Schmidt & Whelan 1998).

Methods

From 1992 to 1997, we studied the nesting success of American Robins and Wood Thrushes in the approximately 200 ha of deciduous woodlands at The Morton Arboretum (15 km west of Chicago, Illinois, U.S.A.) and the abutting 150-ha Hidden Lake Forest Preserve (for site description see Schmidt and Whelan [1998]). We located and monitored nests throughout the breeding season by visual inspection every 2–5 days. We classified successful nests as those that fledged at least one host young, determined by inspection of the nest and surroundings and by the timing of the disappearance of nestlings. Unsuccessful nests often failed due to predation (>95%). We ascribed predation to large mammals (e.g., raccoons) when nests were physically and violently disturbed (e.g., tipped over or knocked out of a tree) or when tracks, fur, scratch marks on bark, and broken branches or stems were conspicuous. We calculated the daily nest mortality rate using Mayfield's (1975) method. We also recorded the nest shrub or tree species for all nests and visually estimated nest height to the

nearest 15 cm for nests ≤ 3 m above the ground and to the nearest 0.5 m for higher nests. We pooled data across years but analyzed DMRs of robins and thrushes separately with the program CONTRAST (Hines & Sauer 1989). Nests placed in dead trees or shrubs, *Rosa multiflora*, and *Celastrus* spp., were excluded from the analyses due to low sample sizes.

Results

We performed pairwise comparisons of daily nest mortality rate (DMR) between nests built in *Lonicera* versus native species (including *Crataegus* and *Viburnum* as well as native tree species, such as *Acer*, *Ostrya*, and *Prunus*) and built in *Rhamnus* versus native species. Nests built in *Lonicera* had significantly higher DMRs than nests in natives for both robins ($\chi^2 = 12.31$, $df = 1$, $p < 0.001$; Fig. 1) and thrushes ($\chi^2 = 4.0$, $df = 1$, $p < 0.05$; Fig. 1), whereas nests built in *Rhamnus* did not have higher DMRs than natives for either species ($p > 0.25$; Fig. 1).

As a potential explanation for these results, we tested for an effect of nest height in robins (thrushes showed too little variability in nest height for an analysis) with regression analysis. Daily mortality rate, calculated from a minimum of five nest attempts per height category, was inversely related to nest height ($r^2 = 0.496$, $p = 0.001$; Fig. 2). Moreover, the proportion (arcsin-square-root-transformed) of depredated nests (minimum of four depredations per height category) ascribed to large

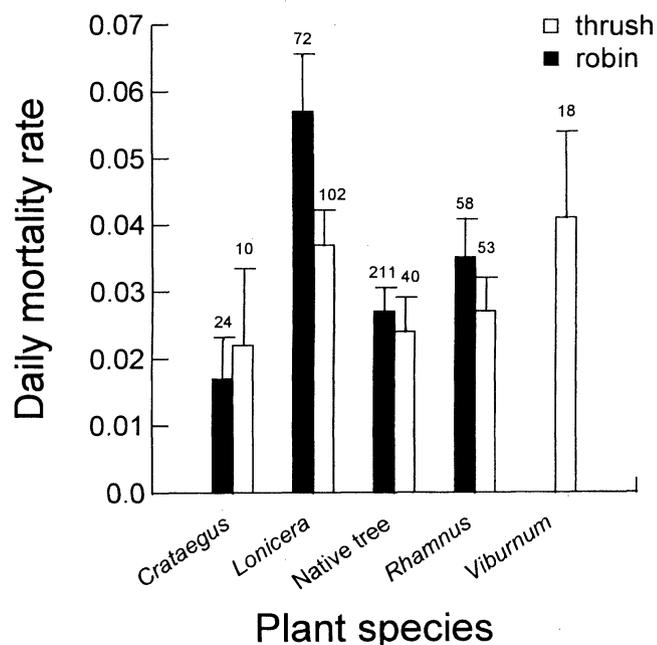


Figure 1. Nest daily mortality rate (DMR ± 1 SE) by nest substrate for American Robin and Wood Thrush. Sample sizes are given above bars.

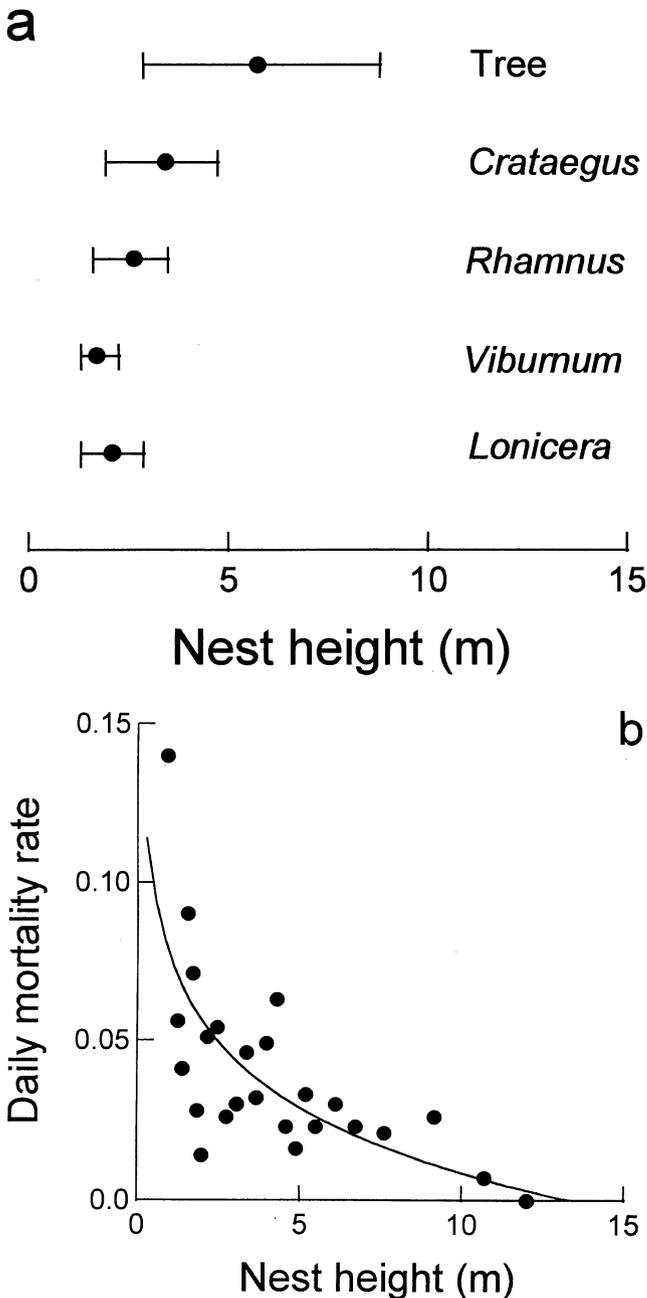


Figure 2. (a) Mean (± 1 SD) height of American Robin nests within the different nest plant species; (b) regression of the daily mortality rate of robin nests against nest height (m). The data fit a logarithmic regression substantially better ($r^2 = 0.496$) than a linear regression ($r^2 = 0.376$).

mammals was also inversely related to nest height ($r^2 = 0.291$, $p = 0.02$).

To control for the effects of nest height in subsequent analyses, we used pairwise comparisons between substrates with strongly overlapping nest height distributions: *Rhamnus* versus *Crataegus* and *Lonicera* versus

Viburnum (Fig. 2a). Sample size considerations constrained the first analysis to robins and the second analysis to thrushes. We tested these comparisons for design differences, such as the absence of long, sharp thorns in *Rhamnus*, and architectural differences, such as sturdy branches or reduced basal cover in *Lonicera*, relative to those of native shrubs of comparable height and stature. We performed separate analyses using either DMRs calculated from all predation events or only those predation events ascribed to large mammals because we hypothesized that the influence of thorns and substrate architecture would have the largest effect on this group of predators. For robins DMRs were higher in *Rhamnus* all predation events when considering ($\chi^2 = 3.94$, $df = 1$, $p < 0.05$; Fig. 1). Furthermore, this difference was more pronounced when predation by only large mammals was considered (*Rhamnus*: DMR = 0.0272 ± 0.0054 ; *Crataegus*: no mammalian predation; $\chi^2 = 7.26$, $df = 1$, $p < 0.01$). For thrushes, DMRs were not significantly different for either comparison ($p > 0.30$).

Despite experiencing higher predation when nesting in *Lonicera*, robins dramatically increased their use of *Lonicera* over the study period ($r^2 = 0.912$, $p < 0.01$; Fig 3a) from 5% in 1992 to 33% in 1997, with a concomitant decline in the use of native trees. Thrushes showed no overall trend ($p > 0.25$), but *Lonicera* was more frequently used in the latter half of the study (Fig. 3a). This increased overlap comes at a cost to thrushes. The DMR of thrush nests built in *Lonicera* was positively related to the annual number of robins nesting in *Lonicera* ($r^2 = 0.462$, $p < 0.07$, 1-tailed test; Fig 3b) and not simply the cumulative number of nests, as previously determined (Schmidt & Whelan 1998).

Discussion

Our data show that exotic *Lonicera* and *Rhamnus* affected songbird nest success in two ways. First, exotic shrubs directly enhanced nest predation (primarily by large mammals) in American Robins, perhaps through a combination of lower nest height, the absence of sharp thorns, and a branch architecture that may facilitate predator movement. Despite higher predation, robins increased their use of *Lonicera* during our study (Fig. 3a). The cause of the increase is unknown but appears related to *Lonicera*'s early leaf flush and expansion (Trisel & Gorchoy 1994). Robins nest in *Lonicera* most often early in the season (K.A.S., unpublished data), although it is unknown whether this is because early leaf flush attracts early-season nesting activity or whether robins choose alternative substrates after attempts in *Lonicera* have failed. The former hypothesis suggests an ecological trap (Gates & Gysel 1978), whereas the latter suggests an adaptive response, although the two behaviors are not mutually exclusive. Other temporal correla-

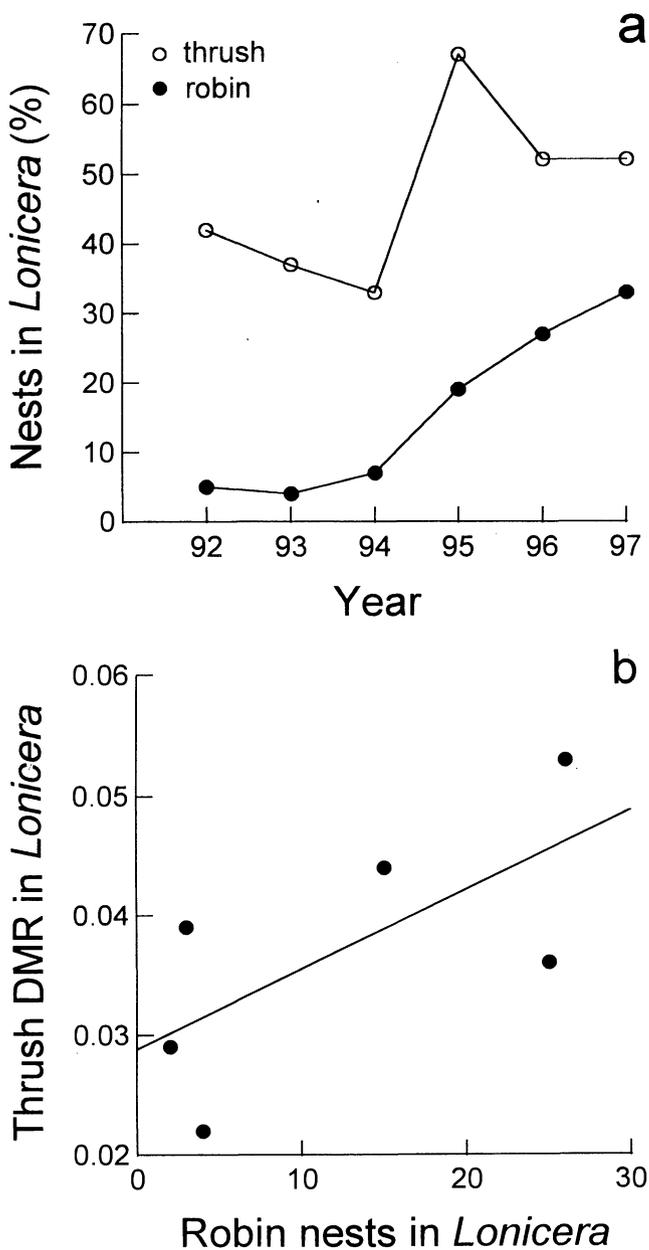


Figure 3. (a) Percentage of annual nest attempts built in *Lonicera* for American Robin and Wood Thrush; (b) regression of daily mortality rate of thrush nests placed in *Lonicera* against the number of robins nesting in *Lonicera*.

tions, such as higher predator activity early in the season (Schmidt 1999), may provide alternative explanations for our results. We recommend experimental tests to fully explore these possible interactions.

Second, predation among nesting Wood Thrushes was higher in *Lonicera* than the pooled native species, but not compared with *Viburnum*, a species of comparable height and stature. Furthermore, predation among thrushes nesting in *Lonicera* was influenced by the

number of robins nesting in *Lonicera* (Fig. 3b). Wood thrushes, which built roughly half their nests in exotics in any given year, experienced apparent competition with robins nesting in *Lonicera* (also see Schmidt & Whelan 1998). These results suggest that *Lonicera* are unfavorable sites for thrush nests due to overlap with nesting robins. This interaction is further exacerbated by two circumstances. First, because robins often reach large population sizes in highly fragmented landscapes, they are perhaps most likely to overlap in breeding habitat with Wood Thrushes in the very landscapes most susceptible to exotic shrub invasion. Second, as indicated above, the early leaf flush of *Lonicera* may be driving the higher overlap with robins.

Currently, our results are specific to a single site and pair of species; it is unknown to what extent they may generalize across a greater geographic or taxonomic range. Neither the direct nor indirect effects of exotic plants on nest predation need be restrictive to exotic species. Furthermore, the relationship between the invasion of exotics and their use by nesting birds is likely dependent on the landscape context. These caveats make it hard to generalize from our findings without further data. Nonetheless, we believe that several important conservation issues will benefit from a more thorough understanding of the relationship between exotic plants and nest predation. First, our investigation underscores the need for accurate measures of fitness and population performance when habitat suitability is assessed. For instance, van Horne (1983) emphasized that population density does not necessarily correlate with habitat quality. Similarly, we show that the frequency of use of a particular plant species for nest sites does not necessarily correlate positively with nesting success (e.g., Martin 1998). In our study system, assuming that the higher frequency with which available plant species were used as nesting substrates is an indication of higher nesting success would lead to the erroneous conclusion that exotic shrubs actually benefit native bird species, a management position that is not only controversial (Whelan & Dilger 1992, 1995) but, upon inspection, wrong.

Second, exotic shrubs may play an important role in fragmented and edge habitats. There is compelling evidence that various songbird species are declining, at least in some portions of their range (Askins et al. 1990; James et al. 1996). Although mechanisms underlying these declines are controversial (Rappole & McDonald 1994; Latta & Baltz 1997), nest predation is a leading candidate (e.g., Robinson et al. 1995). Habitat disturbance and fragmentation exacerbate both nest predation (Robinson et al. 1995) and exotic plant invasion (Hobbs & Huenneke 1992; Hutchinson & Vankat 1997), and we suggest that these phenomena are partly intertwined. Insofar as exotic shrubs are associated with habitat fragmentation and edges, higher predation rates in exotic shrubs, such as we have documented, may be

one cause of the higher predation rates in fragmented landscapes and along habitat edges.

While likely to be controversial, this proposition at least appears feasible, and we hope our results will stimulate critical research in this area. If invasive, exotic shrubs are shown to increase nest predation in other settings, restoring native, fruit-producing shrub species could accomplish several conservation goals simultaneously by enhancing native plant species richness and songbird nest success, while concomitantly maintaining fruit resources necessary for migrant fat deposition.

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