INVASIVE SHRUBS AND SONGBIRD NESTING SUCCESS: EFFECTS OF CLIMATE VARIABILITY AND PREDATOR ABUNDANCE

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Abstract. Previous studies have demonstrated that songbirds often use exotic plants as nesting substrates and may suffer elevated predation rates relative to nests placed in native plants. Veeries (*Catharus fuscescens*) frequently build nests in an exotic shrub, Japanese barberry (*Berberis thunbergii*), in forests of southeastern New York State, USA. We monitored Veery nesting success over a six-year period and supplemented these observations with experimental nests to determine whether predation rates differed between nests placed on the ground, in barberry shrubs, or in alternative native substrates. Using experimental nests, we found that nests raised above the ground in either barberry or native plants survived significantly longer than ground nests, but predation did not differ between the two former sites. Similarly, Veery nests on the ground suffered higher predation rates than nests in either raised native substrates or barberry; however, despite a substantially lower daily mortality rate in barberry, the difference was not significant. The lack of significance is apparently related to temporal variability in substrate or habitat preference by Veeries and strong temporal variation in the assemblage of nest predators. Barberry offered relatively greater refuge from nest predators during outbreaks of rodent populations. Years with higher spring precipitation reduced the use of mesic drainages (where barberry is abundant) for nest sites, and concomitantly fewer nests were placed in barberry. Although the differences in nest predation rates are relatively small, we estimated that nesting in barberry vs. on the ground can cause an ~10% increase in annual fecundity. Thus, strong differences in the density of barberry or chronic changes in climate can have long-term impacts on songbird populations.

Key words: barberry; Berberis thunbergii; Catharus fuscescens; *climatic variability; exotic plants; experimental nests; invasive shrub; nest predation; Veery; white-footed mouse.*

INTRODUCTION

The impact of invasive, exotic, or nonnative species on communities has received increasing attention in recent years (Daehler and Strong 1983, Drake et al. 1989, Hobbs and Huenneke 1992, Lodge 1993*a, b,* Louda et al. 1997, Rabenold et al. 1998, Mack et al. 2000, Sakai et al. 2001, Alvarez and Cushman 2002, Sanders et al. 2003), as exotic species have increasingly invaded communities around the world. Much of the current research has focused on understanding the characteristics of invading species (or the habitats they invade) that lead to their success (Daehler and Strong 1983, Elton 1958, Lodge 1993*a, b,* Sakai et al. 2001). A second line of inquiry has examined the consequences of invasion on the characteristics of the resulting community (Vitousek and Walker 1989, Hobbs and Huenneke 1992, Whelan and Dilger 1992, Schmidt and Whelan 1999*a,* Alvarez and Cushman 2002, Sanders

et al. 2003). Exotics often have detrimental direct and indirect effects on the native flora and fauna in areas that they have invaded (Drake et al. 1989, MacDonald et al. 1989, Soulé 1990, Westman 1990, Mack et al. 2000), with sometimes disastrous consequences to native communities (e.g., Vitousek and Walker 1989, Sanders et al. 2003).

Less obvious impacts from the invasion of exotic species may occur when exotics apparently blend into native communities and other animals and plants use the exotic species in similar ways to the native species that they have replaced. For example, Whelan and Dilger (1992, 1995) documented the use of invasive, nonnative shrubs, particularly *Lonicera maackii* and *Rhamnus cathartica,* as nest sites by temperate forest songbirds. *Rhamnus,* in particular, was strongly associated with American Robin (*Turdus migratorius*) territories, suggesting that it may have a beneficial role. However, Schmidt and Whelan (1999*a*) later showed that these nonnative shrubs resulted in decreased fecundity in American Robins and Wood Thrushes (*Hylocichla mustelina*) breeding in Illinois. Further documentation of negative impacts of exotic species on avian breeding success has followed in recent years (Remeš 2003, Borgmann and Rodewald 2004).

Nonnative trees and shrubs, e.g., *Lonicera* spp., *Rhamnus* spp., and *Rosa multiflora*, have invaded numerous states throughout the United States (Luken and Thieret 1996, Hutchinson and Vankat 1997), with a diverse set of consequences for avian communities, including reduced species abundance and community diversity, and higher reproductive failure. The mechanisms for these relationships have not been thoroughly explored, but include increased brood parasitism (Reichard et al. 2001) and nest predation through direct and indirect (i.e., apparent competition) means (Schmidt and Whelan 1999*a*, Remeš 2003, Borgmann and Rodewald 2004). Furthermore, exotics have been implicated in generating edge effects in forested habitat and they may serve as ecological traps (Gates and Gysel 1978, Schmidt and Whelan 1999*a*). Ultimately, the invasion of exotic plants may serve as a potential mechanism driving declines in some songbird populations or in avian community diversity. For instance, studies have found that native bird species diversity and density correlated negatively with the volume of exotic vegetation in Arizona (Mills et al. 1989, Germaine et al. 1998) and California (Rottenborn 1999). Likewise, Seaside Sparrow (*Ammodramus caudacutus*) and Saltmarsh Sharp-tailed Sparrow (*Catoptrophorus semtipalmatus*) abundance was reduced in marshes dominated by *Phragmites* (Benoit and Askins 1999). The presence of exotic species is also linked to variation in the composition of foraging guilds. For instance, compared to stands of native cottonwood (*Populus fermontii*), stands invaded by saltcedar (*Tamarix*) supported reduced diversity and abundance of Neotropical migrant songbirds (Ellis 1995, Hunter et al. 1998).

In this study, we compared nest predation rates on Veeries (*Catharus fuscescens*) nesting in an exotic shrub, Japanese barberry (*Berberis thunbergii*), to predation on nests in native substrates. Veeries breed in humid deciduous forest, where they nest in low shrubs or directly on the ground. Japanese barberry is a low, densely foliated, thorny shrub (Johnson 1996) that has been used as an ornamental plant throughout the United States. It has escaped cultivation and invaded many forested areas in the East Coast and Midwest (Wohl 1995, Ehrenfeld 1997). Despite the fact that barberry does not appear to mimic the structure of native shrubs within temperate forests of the northeastern United States, it frequently has been used as a nesting substrate by Veeries. Because Veeries have been experiencing population declines in the eastern United States (Sauer et al. 1997), determining how barberry affects songbird breeding productivity may have important management implications.

STUDY AREA AND METHODS

Study area

Field studies were conducted on the property of the Institute of Ecosystem Studies (IES) in Dutchess County, southeastern New York State, USA. IES property includes ~325 ha of continuous eastern deciduous forest dominated by oaks (*Quercus rubra* and *Q. prinus*) in the canopy, and with oaks, sugar maple (*Acer saccharum*), eastern hemlock (*Tsuga canadensis*), maple-leaved viburnum (*Viburnum acerifolium*), and witch-hazel (*Hamamelis virginiana*) common in the understory.

Observations of natural nests

We monitored Veery nests from 1998 to 2003 following standard protocols (Martin and Geupel 1993). Veeries built nests in a variety of locations. At a coarse level, we recognized three substrate choices: (1) nests built on or close (<20 cm) to ground; the latter nests were often slightly raised when placed at the base of a multi-stemmed plant; (2) above ground in barberry or multiflora rose, which share similar architecture and possess small, sharp thorns; and (3) above ground (20–100 cm) in a native plant. Nests were also more finely classified based on our own perceptions and search images developed while searching for nests. These categories may be somewhat subjective, but because they are often defined by plant- or habitat-specific associations, Veeries may be responding to the particular features that we also recognized. These categories include: (1) barberry; (2) *Vaccinium* spp.; (3) base of *Lonicera* stems; (4) maple-leaf viburnum; (5) brushpiles consisting of dead branches; (6) grass tussocks in or surrounding permanent water pools; (7) sucker growth, usually along the lower trunk of *Fagus grandifolia*, *Carpinus caroliniana*, or *Castanea dentata*; (8) directly on the ground in the open or under a woody stem; and (9) other. We categorized the locations of all nests by plant association, measured the height from the ground to the rim of the nest, and examined the number and percentage of nests fledging by category.

Veery nests are highly vulnerable to small mammals (Schmidt and Ostfeld 2003) that forage mainly on the ground and may avoid barberry due to the presence of thorns, whereas larger mammalian (e.g., raccoon) and avian predators would not be deterred by these characteristics. Because our oak-dominated study site is characterized by extreme annual variability in rodent densities (Schmidt and Ostfeld 2003), the potential for barberry to provide a refuge from rodent nest predation may also fluctuate between years in relation to the abundance of small mammals. To test this, we logarithmically transformed the ratio of daily mortality rates (DMRs) of barberry to non-barberry nests for both real nests (excluding years 1998 and 2000, in which sample sizes were <5 for some categories) and artificial nests (1999, 2002, 2003) as the dependent variable. DMR is calculated by dividing the number of depredated nests by the total number of nest exposure days (Mayfield 1975). Preliminary analysis revealed no effect of nest type ($F_{1,4} < 0.02$, $P > 0.80$); therefore, we pooled the data and used linear regression analysis be-

tween the ratio of DMRs and rodent density (for enumeration of rodent densities, see Jones et al. 1998, Schmidt and Ostfeld 2003).

If barberry offers protection against rodent predation as previously hypothesized, Veeries may assess nest predation risks and may respond accordingly by building more nests in barberry during high rodent years. Alternatively, preferences for nest microsites may vary in response to climatic variation (e.g., Martin 2001). In particular, barberry tends to be most abundant in mesic drainages that often contain permanent pools of water. During wet years, these pools expand and may threaten to flood nest sites, causing Veeries to shift toward well-drained slopes where barberry seldom grows. Therefore, we tested whether the annual proportion of nests in barberry and in mesic drainages varied with spring (April plus May) precipitation, the time of year most likely to influence nest building, which is typically completed by early-to-mid June. We examined the relationship between the proportion of nests placed in barberry or above ground (the latter also includes non-barberry substrates) against rodent density using linear regression and against spring precipitation using Pearson correlation. Precipitation data were downloaded from the IES weather station. Inactive Veery nests (i.e., those fledged or attacked prior to our finding the nests) were included in the calculations of substrate choice, but not the variables regarding nest success (e.g., DMR); therefore sample sizes may change between analyses.

Artificial nest experiments

General.—We conducted three artificial nest experiments (1999, 2002, and 2003) to complement our observations of Veery nests. All experiments followed a similar protocol that consisted of using clay eggs, shaped and sized to resemble a Veery egg, within artificial stick nests. There were slight differences between experimental protocols; however, because comparisons are only conducted within years, these are not of statistical concern. For instance, in 1999, we minimized human scent by handling all nests and eggs with latex gloves, whereas in later years, clay eggs were coated with a thin layer of unscented beeswax to eliminate the earthy odor of clay, at least to humans. Regardless, predation rates did not differ between nests with and without a clay egg in an initial sample of 40 nests (20 containing only a single Zebra Finch (*Taeniopygia guttata*) egg and 20 containing a single clay egg) used in the 1999 experiment ($P > 0.15$). Likewise, Schmidt et al. (2001) concluded from their earlier experiments in this system that the artificial nests and the presence of either clay or Zebra Finch eggs did not influence nest predation rates. In all experiments, we waited two days from the initial placement of nests in the field before baiting them with eggs, and we avoided the use of insect repellent at all times.

In 1999 we checked nests every two days (14 days in total) for the presence of eggs and examined them for signs of predation. If eggs were missing, damaged, or contained tooth imprints, the nest was considered to be depredated. This classification was used in later experiments as well; however, nests were inspected the day after baiting and every three days thereafter for a total of 16 days. We calculated that the nest daily mortality rate using Mayfield's (1975) method and assuming that the timing of predation events occurred on the second day of exposure (experiment 1) or midway between the last and previous nest check (experiments 2 and 3). We calculated the variance following Johnson's (1979) procedure and used the program CONTRAST (Hines and Sauer 1989) for pairwise comparisons of DMRs.

Experiment 1.—We placed nests in three different locations: barberry, oak saplings, and on the ground. Nests in either barberry or oak saplings were placed 25–40 cm off the forest floor in microhabitats similar to those used in natural Veery nests. Because patches of oak saplings and barberry grow within different microhabitats (oak saplings are often found in moderately or well-drained slopes, whereas barberry is common in mesic drainages), we could not directly compare nest predation rates among the three substrates while simultaneously controlling for microhabitat. Therefore, we placed nests in pairs, with each barberry or oak sapling nest paired to a ground nest (''barberry ground'' and ''oak ground'' nests) placed no more than 25 m away. Replicate pairs were spaced at least 50 m apart and with the dates of initiation staggered so that, in total, 47 replicates (23 oak, 24 barberry; one was lost, leaving 46 for analysis) were initiated between 23 June and 10 July 1999. Nests were picked up after depredation or 14 days of exposure. We calculated DMRs separately for barberry, barberry ground, oak sapling, and oak ground nests. We conducted pairwise comparisons using the program CONTRAST between ground nests within each treatment (barberry and oak), between ground nests across treatments, and between raised nests across treatments.

Experiments 2 and 3.—Experiments 2 and 3 were designed to tease apart habitat-specific nest predation rates. In particular, natural Veery nesting data suggested that lowland sites (depressions where water can collect following large precipitation events or low areas near a slow-moving or stagnant, permanent body of water) experienced higher nest predation than upland sites (peaks or slopes of hills or ridges characterized by greater amounts of sunlight and dry soil conditions). Between 9 and 30 June 2002, we placed a total of 90 artificial nests equally divided into six treatments: two habitats (lowland vs. upland) × three substrates (directly on the ground at the base of a shrub, sapling, or in a tuft of grass; 15–45 cm above ground in barberry; 15–45 above ground in a non-barberry substrate). Experiment 3 followed the identical protocol; however,
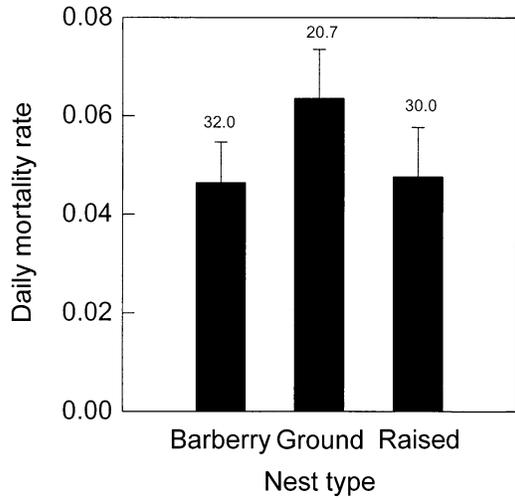
FIG. 1. Nest daily mortality rates (mean ± 1 SE) on Veery nests during our six-year study. Numbers above each bar give the percentage of nests surviving over a 24-day nest cycle.
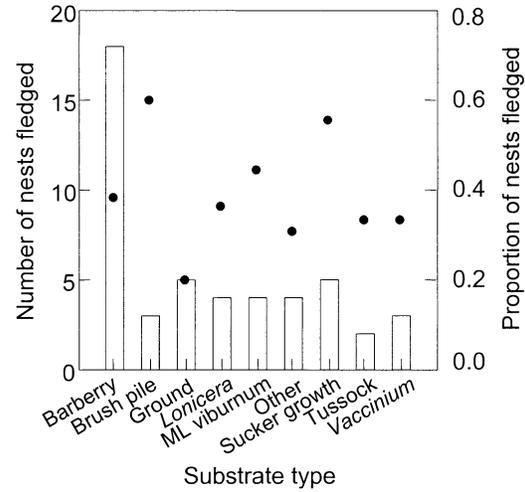

FIG. 2. Number of nests fledged (bars) and proportion of nests fledged (solid circles) by substrate category. All categories had sample sizes ≤13 except barberry ($n = 47$) and ground nests ($n = 25$). "ML viburnum" indicates maple-leaf viburnum.

all nests were placed out on the same date, 26 June 2003.

RESULTS

Natural nests

We monitored a total of 143 active Veery nests over a six-year period. We placed 44 nests in barberry and five in multiflora rose; 36 nests were placed in other raised substrates (30–50 cm above ground), and 55 nests were placed on or slightly (<10 cm) above ground. Two additional nests had no substrate recorded and one nest was built on top of a small-mammal enclosure fence! Veery nests in barberry had lower nest predation rates than nests placed on the ground (Fig. 1; DMR = 0.0464 or 68.0% of nests vs. 0.0635 or 79.3% of nests), but this difference was not statistically significant ($\chi^2 = 1.73$, df = 1, $P = 0.181$). Nest predation rates in alternative raised substrates were similar to those of barberry nests (Fig. 1; DMR = 0.0476 or 70.0% of nests).

Substrate choice

Veeries built nests more often in barberry than in any other class of substrate that we recognized (Fig. 2). Ground nests were second; nests in this category include both nests built in the open and those built under a sapling or small tree, but exclude nests built in grass tussocks near the edge of permanent water. More nests fledged from barberry than any other substrate (Fig. 2). In terms of percentage of nest success, barberry appeared about average, although most categories contain too few nests for a rigorous comparison. The one exception is ground nests, which fledged only 20.0% of 25 nests as compared with 38.4% of 47 nests in barberry/multiflora rose, although this difference is not significant (Fisher's exact test $P = 0.122$).

Temporal variability in substrate choice and nest predation rates

The ratio of daily mortality rates of barberry to non-barberry nests was negatively related to the annual density of rodents ($r^2 = 0.641$, $P = 0.031$; Fig. 3). In other words, nests built in barberry had lower predation rates relative to alternative substrates during years with higher densities of rodents. Veeries did not build a greater proportion of nests in barberry ($r^2 = 0.017$, $P > 0.80$) or above ground ($r^2 = 0.106$, $P > 0.50$) during high
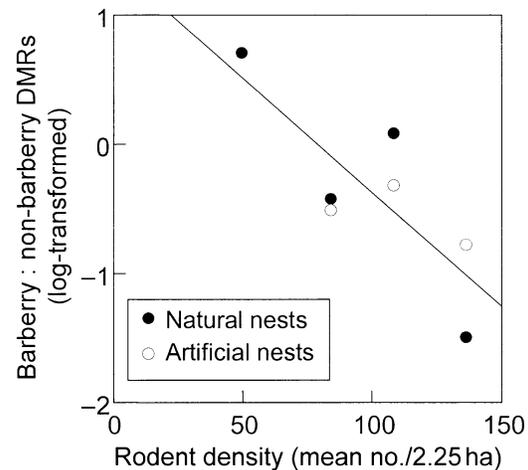

FIG. 3. Relative predation rates on barberry nests, expressed as the ratio of barberry : non-barberry nests, as a function of annual rodent density. Rodent density (white-footed mouse and eastern chipmunk) was computed from six 2.25-ha trapping grids (see Jones et al. 1998, Schmidt and Ostfeld 2003), with the exception of 2003 chipmunk densities, which were extrapolated based on previous 5-year regression between mouse and chipmunk densities.
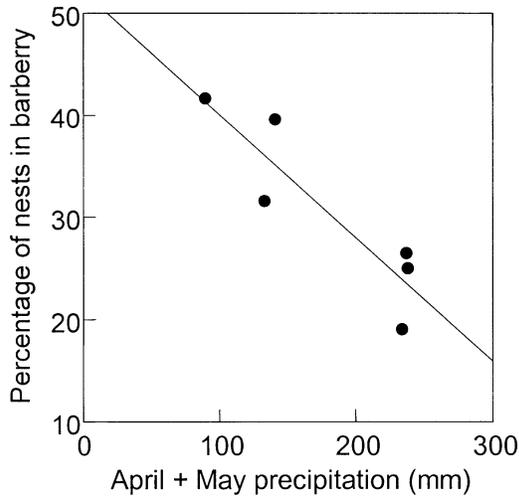
Fig. 4. Annual percentage of nests placed in barberry as a function of spring (April + May) precipitation.

rodent years. However, the annual percentage of Veery nests built in mesic drainages varied inversely with the sum of April and May precipitation ($r^2 = 0.559$, $P = 0.044$; one-tailed test). Likewise, the annual percentage of Veery nests built in barberry, but not in all raised substrates, varied with precipitation (Fig. 4; for barberry, $r = -0.897$, $P < 0.05$; for all raised substrates, $r = 0.017$, $P > 0.80$). In wet years, Veeries move out of mesic drainages where their nest site selection is more constrained (i.e., by a lack of barberry).

Artificial nest experiments

1999.—Nests in both barberry and oak saplings had lower predation rates than their paired ground nests (barberry, $\chi^2 = 9.72$, df = 1, $P < 0.01$; oak, $\chi^2 = 16.3$. df = 1, $P < 0.001$). There was no statistical difference in DMRs between ground nests in the oak and barberry treatments ($\chi^2 < 0.1$, df = 1, $P > 0.90$). Likewise, DMRs did not differ between raised nests in the oak and barberry treatments ($\chi^2 = 1.83$, df = 1, $P > 0.20$; see Table 1).

2002.—Predation rates on lowland nests were extremely high (~30% per day) and we conservatively decided to drop them from the analysis of DMRs. Among uplands nests, differences in predation rates

between barberry and alternative raised substrates were not significant ($\chi_1^2 < 0.10$, $P = 0.83$). In the comparisons between ground nests and raised substrates, barberry and alternatives, the marginally nonsignificant trend was toward higher predation rates on ground nests ($\chi_1^2 = 2.81$, $P = 0.094$ and $\chi_1^2 = 3.43$, $P = 0.064$, respectively; see Table 1).

2003.—There were no differences between lowland and upland nests ($\chi_1^2 = 1.431$, $P = 0.23$) or among substrates in the lowlands ($\chi_1^2 = 0.13$, $P = 0.72$). Upland nests placed in barberry had significantly lower predation rates than ground nests ($\chi_1^2 = 7.74$, $P = 0.0054$) and nearly significantly lower predation rates than alternative raised-substrate nests ($\chi_1^2 = 3.69$, $P = 0.055$; see Table 1).

Predator identification

In total, 53 of 273 artificial nests survived, the majority of which were placed in barberry (21 of 84 = 25%) and alternative raised substrates (23 of 83 = 27.7%), whereas ground nests had extremely poor survivorship (9 of 106 = 8.5%). White-footed mice were the dominant predator (52.3% of depredated nests), followed by chipmunks (11.4%) and raccoons (5.5%), with the remainder unidentified largely due to missing eggs.

DISCUSSION

Using experimental nests, we demonstrated that nests in barberry shrubs had lower predation rates than nests on the ground, whereas predation rates on raised nests (whether in barberry or alternative native substrates) were comparable; there was a single exception (2003 upland nests) in which lower predation rates in barberry compared with other raised nests approached statistical significance ($P = 0.055$). Nearly identical patterns of predation were observed among real Veery nests. However, despite considerably higher daily mortality rates on Veery ground nests, differences were not statistically significant. We believe that the trend is real, but that the average high predation (~73% of nests between 1998 and 2003), extreme temporal variability in the relative abundance of nest predators (Schmidt and Ostfeld 2003), and uncontrolled site (e.g., lowland vs. upland) and year differences reduced our ability to

TABLE 1. Daily mortality rates (with 1 SE in parentheses) on experimental nests by year and by category.

Experimental nests	1999	2002, upland nests	2003	
			Upland nests	Lowland nests
Barberry	0.1084 (0.0245)			
Ground paired with barberry	0.2857 (0.0515)			
Oak sapling	0.0677 (0.0181)			
Ground paired with oak	0.2899 (0.0520)			
Barberry		0.1158 (0.0011)	0.0513 (0.0223)	0.0690 (0.0342)
Ground		0.2222 (0.0030)	0.1942 (0.0605)	0.1183 (0.0393)
Raised		0.1058 (0.0010)	0.1258 (0.0415)	0.0529 (0.0266)

Note: Data for 2002 lowland nests were not analyzed because predation rates were very high and considered unrealistic.

detect an effect. For instance, rodents were the most important predators on experimental nests, and this apparently holds for real nests as well (Schmidt and Ostfeld 2003). However, rodent populations fluctuated between ~10 and 70 individuals/ha over the six years of our study (Schmidt and Ostfeld 2003). We suggest that the real nest data collected over this time period should show variable trends in the percentage of barberry nests depredated. Indeed, the relative predation rate on barberry nests is inversely proportional to rodent abundance; in years with higher rodent densities, barberry offers relatively greater safety from nest predators. We suspect that rodents rarely forage within barberry and thus do not encounter nests frequently, whereas other predators, e.g., raccoons or raptors, can more easily consume a nest without the need to climb within its thorny branches.

Substrate use also suggests that barberry is important for Veery nesting success. Over our 6-year study, Veeries nested more frequently in barberry than in any other substrate. Over 37% (18 of 48) of all successful nests were placed in barberry, and barberry nests had nearly twice the fledging success as the next most frequent class (using the finer categorization) of substrate types, i.e., ground nests. Thus sites where barberry is rare or absent may be less productive than sites containing barberry. However, to confirm this would require an understanding of how Veeries select nest sites and territories in barberry-free areas.

Our results differ from those of Schmidt and Whelan (1999a) from the perspective of comparing nest predation rates between nests placed in native and exotic plants. Schmidt and Whelan interpreted the higher predation rates on nests in exotics plants as due to: (1) low stature of exotic shrubs and the closer proximity of the nest to the ground; (2) the absence of physical deterrents (i.e., long, sturdy thorns) that occurred in natives; and (3) a branch architecture that facilitated access to the nest by medium-sized mammals, such as raccoons. In the current study, it is barberry that possesses numerous sharp thorns and results in greater nests heights, features that may deter small ground-foraging rodents. We suggest that it is specific physical traits of plants, rather than their status as exotics, per se, that determine their effect on nesting success.

Effect size

We suggest that barberry provides some refuge from nest predation, but that this benefit fluctuates annually in relation to the relative densities of various nest predators. The difference in seasonal fecundity between 69% predation (barberry nests) and 80% predation (ground nests) is 0.619 young/female (using the observed mean fecundity per successful nest, 3.375 chicks, and assuming that Veeries build two replacement nests if earlier nests are depredated; see Schmidt and Whelan 1999b). Assuming a 1:1 sex ratio and 35% juvenile survivorship, this difference corresponds to a 0.108 increase in juvenile recruitment, on average, from nests in barberry as compared to nests on the ground. Climatic conditions also influence the magnitude of this effect, because Veeries are more likely to nest in barberry during dry springs. A 20% shift (see Fig. 4) toward more frequent nesting in barberry would result in a 2% change in growth rate, on average, given the nest predation rates that we used. As indicated earlier, the benefit during individual years will depend on the relative abundances of nest predators. Nonetheless, these calculations provide an index for estimating the influence of chronic climate changes on Veery populations in areas invaded by barberry. All else equal, wetter springs will result in a drop in productivity that must be ameliorated or compensated by other means.

Are exotics sometimes beneficial?

Despite the fact that barberry provides an apparently plentiful and relatively high-quality nesting substrate at our site, particularly against rodent predation, the net effects of this exotic shrub on Veery population dynamics cannot yet be determined for several reasons. First, exotic species usually will impose a mixture of positive and negative effects at a community level. In particular, rates of nutrient cycling are enhanced under barberry and this, in turn, facilitates the invasion of exotic earthworms into areas where barberry has become established (Ehrenfeld 1997). These changes may bring about dramatic shifts in avian communities much like the shifts in guild composition noted in other sites (Fraser and Crowe 1990, Ellis 1995). For instance, barberry invasion may favor ground-foraging species that consume the greater soil invertebrate biomass associated with barberry, at the expense of foliage gleaners. We have observed that heavily invaded sections of the forest where this study was conducted tend to support few Veeries. In fact, Veeries appear to prefer isolated barberry plants rather than large clusters (K. A. Schmidt, *personal observation*), suggesting that an initial beneficial effect of barberry on Veeries may shift to a strong negative effect during a continually expanding invasion.

In conclusion, our study strongly suggests that differential nesting success is linked to fluctuation in the assemblage of predators, with higher relative nesting success in barberry during years with greater densities of small rodents, although overall predation rates are higher in these years regardless of substrate choice (Schmidt and Ostfeld 2003). Second, nest site decisions are variable and the choices have meaningful consequences. If nest site selection is heritable, a 0.108 increase in juvenile recruitment to adulthood should lead to rapid evolution toward nesting in barberry. This may explain the heavy use of this recently invaded shrub that apparently lacks a native counterpart in terms of structure. Third, nest site choices are often correlated with weather patterns, suggesting that chronic climate change can yield important long-term consequences for

songbird populations. This point has been stressed by a number of studies linking higher nest predation rates to changes in substrate choice mediated by climate variability. Nest predation rates increased as species shifted to nesting in less preferred vegetation zones (Martin 2001) or toward heavier use of exotic plants (suggesting synergistic effects of weather and species invasion) that have relatively earlier leaf flush, particularly in cool springs, than do native species (Schmidt and Whelan 1999*a*, Remeš 2003).

The conservation implications of effects due to climate change and species invasion (and synergisms between these factors) are far reaching. Songbirds are known to quickly adapt to and begin using exotic plants as nesting substrates (Whelan and Dilger 1992). The few studies to date that have examined the effects of exotic plants on nesting success present a mixed bag of results, demonstrating both negative (i.e., exotic plants as ecological traps; Gates and Gysel 1978, Schmidt and Whelan 1999*a*) and positive influences (this study). With the present exception, no studies to date have conducted a lengthy study to quantify interactive effects due to variability in weather and/or predator abundance. Our study suggests linkages between biotic and abiotic variables such that predicting the long-term influences of invasive species on native communities may be difficult. We stress the urgency for documenting long-term effects of invasive and exotic plant species on avian nesting success, or other demographic components, by quantifying their demographic costs. Also urgently needed are studies that examine the effects of exotics plants on songbirds across a gradient of invasion (e.g., time since invasion) to determine how demographic costs (or benefits) vary quantitatively and qualitatively throughout a continual invasion process. For instance, the appearance that Veeries avoid larger (older?) clusters of barberry begs follow-up studies that, until completed, limit the long-term application of our work to management of Veery populations.

Literature Cited

Alvarez, M. E., and J. H. Cushman. 2002. Community-level consequences of a plant invasion: effects on three habitats in coastal California. Ecological Applications **12**:1434–1444.

Benoit, L. K., and R. A. Askins. 1999. Impacts of the spread of *Phragmites* on the distribution of birds in Connecticut tidal marshes. Wetlands **19**:194–208.

Borgmann, K. L., and A. D. Rodewald. 2004. Nest predation in an urbanizing landscape: the role of exotic shrubs. Ecological Applications **14**, *in press*.

Daehler, C. C., and J. D. R. Strong. 1983. Prediction and biological invasion. Trends in Ecology and Evolution **8**: 380–381.

Drake, J. A., H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson. 1989. Biological invasion: a global perspective. John Wiley, Chichester, UK.

Ehrenfeld, J. G. 1997. Invasion of deciduous forest preserves in the New York metropolitan region by Japanese barberry (*Berberis thunbergii* DC.). Journal of the Torrey Botanical Society **124**:210–215.

Ellis, L. M. 1995. Bird use of saltcedar and cottonwood vegetation in the Middle Rio Grande Valley of New Mexico, U.S.A. Journal of Arid Environments **30**:339–349.

Elton, C. S. 1958. The ecology of invasions of animals and plants. Chapman and Hall, New York, New York, USA.

Fraser, M. W., and T. M. Crowe. 1990. Effects of alien woody plant invasion on the birds of mountain Fynbos in the Cape of Good Hope Nature Reserve. South African Journal of Zoology **25**:97–108.

Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field–forest ecotones. Ecology **59**: 871–883.

Germaine, S. S., S. S. Rosenstock, R. E. Schweinsberg, and W. S. Richardson. 1998. Relationships among breeding birds, habitat, and residential development in greater Tuscon, Arizona. Ecological Applications **8**:680–691.

Hines, J. E., and J. R. Sauer. 1989. Program CONTRAST: a general program for the analysis of several survival or recovery estimates. USFWS Technical Report 24. U.S. Fish and Wildlife Service, Laurel, Maryland, USA.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology **6**:324–337.

Hunter, W. C., R. D. Ohmart, and B. W. Anderson. 1998. Use of exotic saltcedar (*Tamarix chinensis*) by birds in arid riparian systems. Condor **90**:113–123.

Hutchinson, T. F., and J. L. Vankat. 1997. Invasibility and effects of amur honeysuckle in southwestern Ohio forests. Conservation Biology **11**:1117–1124.

Johnson, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk **96**:651–661.

Johnson, E. 1996. *Berberis thunbergii*, Japanese Barberry. Page 47 *in* J. M. Randall and J. Marinclli, editors. Invasive plants: weeds of the global garden. Brooklyn Botanic Garden Publications, Brooklyn, New York, USA.

Jones, C. G., R. S. Ostfeld, M. P. Richard, E. M. Schauber, and J. O. Wolff. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease dynamics. Science **279**:1023–1026.

Lodge, D. M. 1993*a*. Biological invasions: lessons for ecology. Trends in Ecology and Evolution **8**:133–137.

Lodge, D. M. 1993*b*. Reply from David Lodge. Trends in Ecology and Evolution **8**:380–381.

Louda, S. M., D. Kendall, J. Connor, and D. Simberloff. 1997. Ecological effects of an insect introduced for the biological control of weeds. Science **277**:1088–1090.

Luken, J. O., and J. W. Thieret. 1996. Amur honeysuckle, its fall from grace. BioScience **46**:18–24.

MacDonald, I. A., L. L. Loope, M. B. Usher, and O. Hamann. 1989. Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective. Pages 299–311 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson,

editors. Biological invasion: a global perspective. John Wiley, Chichester, UK.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazza. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications **10**:689–710.

Martin, T. E. 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? Ecology **82**:175–188.

Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology **64**:507–519.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin **87**:456–466.

Mills, G. S., J. B. Dunning, Jr., and K. M. Bates. 1989. Effects of urbanization on breeding bird community structure in southwestern desert habitats. Condor **91**:461–428.

Rabenold, K. N., P. T. Tauth, B. W. Goodner, J. A. Sadowski, and P. G. Parker. 1998. Response of avian communities to disturbance by an exotic insect in spruce–fir forests of the southern Appalachians. Conservation Biology **12**:177–189.

Reichard, S. H., L. Chalker-Scott, and S. Buchanan. 2001. Interactions among nonnative plants and birds. Pages 179–223 *in* J. M. Marzluff, R. Bowman, and R. Donnelly, editors. Avian ecology and conservation in an urbanizing world. Kluwer Academic, Boston, Massachusetts, USA.

Remeš, V. 2003. Effects of exotic habitat on nesting success, territory density, and settlement patterns in the Blackcap (*Sylvia atricapilla*). Conservation Biology **17**:1127–1133.

Rottenborn, S. C. 1999. Predicting the impacts of urbanization on riparian bird communities. Biological Conservation **88**:289–299.

Sakai, A. K., et al. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics **32**:305–332.

Sanders, N. J., N. J. Gotelli, N. E. Heller, and D. M. Gordon. 2003. Community disassembly by an invasive species. Proceedings of the National Academy of Sciences (USA) **100**:2474–2477.

Sauer, J. R., J. E. Hines, G. Gough, I. Thomas, and B. G. Peterjohn. 1997. The North American Breeding Bird Survey results and analysis. Version 96.4. Patuxent Wildlife Research Center, Laurel, Maryland, USA. ⟨http://www.mbr-pwrc.usgs.gov/bbs/⟩

Schmidt, K. A., J. Goheen, R. Naumann, R. S. Ostfeld, E. M. Schauber, and A. Berkowitz. 2001. Experimental removals of strong and weak predators: mice and chipmunks preying on songbird nests. Ecology **82**:2927–2936.

Schmidt, K. A., and R. S. Ostfeld. 2003. Songbird populations in fluctuating environments: nest predator responses to pulsed resources. Ecology **84**:406–415.

Schmidt, K. A., and C. J. Whelan. 1999*a*. Effects of exotic *Lonicera* and *Rhamnus* on songbird nest predation. Conservation Biology **13**:1502–1506.

Schmidt, K. A., and C. J. Whelan. 1999*b*. Seasonal fecundity in songbirds: can abandonment, renesting, and double brooding ameliorate high nest predation and brood parasitism? Conservation Biology **13**:46–57.

Soulé, M. E. 1990. The onslaught of alien species and other challenges in the coming decades. Conservation Biology **4**:233–239.

Vitousek, P. M., and L. R. Walker. 1989. Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, and ecosystem effects. Ecological Monographs **59**:247–265.

Westman, W. E. 1990. Park management of exotic plant species: problems and issues. Conservation Biology **4**:251–259.

Whelan, C. J., and M. L. Dilger. 1992. Invasive, exotic shrubs: a paradox for natural area managers? Natural Areas Journal **12**:109–110.

Whelan, C. J., and M. L. Dilger. 1995. Exotic invasive shrubs: a paradox revisited. Natural Areas Journal **15**:296.

Wohl, N. 1995. Density and distribution of Japanese barberry (*Berberis thunbergii*), an exotic shrub species naturalized in the Morristown National Historical Park, Morris County, New Jersey. Bulletin of the New Jersey Academy of Science **39**:1–5.