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RESEARCH ARTICLE

Evaluating exotic plants as evolutionary traps for nesting Veeries

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ABSTRACT

Human-induced rapid environmental change, such as the introduction of exotic species, can create novel species interactions that might be detrimental to native organisms. For birds, introduced plant species may represent potentially attractive, but dangerous, locations to place a nest. If the environmental cues that birds use to select safe nest sites are unreliable when they apply to nonnative plant species, these plants could act as evolutionary traps: preferred nest substrates that confer the poorest reproductive outcomes. We tested this possibility by assessing reproductive consequences of nest substrate preference in the Veery (*Catharus fuscescens*). We followed the fates of nests in native plants and in three nonnative plants associated with reduced nest success in previous studies (Amur honeysuckle [*Lonicera maackii*], multiflora rose [*Rosa multiflora*], and Japanese barberry [*Berberis thunbergii*]). Veeries preferred to locate nests in nonnative plants and in denser patches of vegetation more dominated by nonnative plants. Nests placed in nonnative plants were more visually concealed. We found no evidence that these preferences were maladaptive, as there was no difference in the daily survival probability of nests based on nest-site characteristics. Veeries were not victims of an 'oviposition trap' in this forest system during the period of our study, but rather were facultatively exploiting nonnative plants to their reproductive advantage.

Keywords: ecological trap, maladaptation, nest-site selection, conservation biology, invasive species

Plantas exóticas como trampas evolutivas para individuos anidantes de *Catharus fuscescens*

RESUMEN

Los cambios ambientales rápidos causados por los humanos, tales como la introducción de especies exóticas, pueden crear nuevas interacciones entre especies que podrían ser perjudiciales para los organismos nativos. Para las aves, las especies de plantas introducidas podrían representar un atractivo potencial, pero podrían ser sitios peligrosos para construir sus nidos. Si las señales ambientales que usan las aves para seleccionar sitios seguros para anidar no son confiables cuando se aplican a las plantas no nativas, dichas plantas podrían actuar como trampas evolutivas siendo sitios de anidación preferidos pero que confieren pobres resultados reproductivos. Evaluamos esta posibilidad determinando las consecuencias reproductivas de las preferencias por sustratos de anidación en *Catharus fuscescens*. Seguimos el destino de nidos en plantas nativas y en tres plantas no nativas asociadas con la reducción en el éxito de los nidos en estudios previos (*Lonicera maackii*, *Rosa multiflora* y *Beberis thunbergii*). *C. fuscescens* prefirió ubicar sus nidos en plantas no nativas y en parches de vegetación más densos y dominados por plantas no nativas. Los nidos ubicados en plantas no nativas estaban visualmente más escondidos. No encontramos evidencia de que estas preferencias fuesen maladaptativas, ya que no hubo diferencias en la probabilidad de supervivencia diaria de los nidos basadas en las características del sitio de anidación. *C. fuscescens* no es una víctima de la 'trampa de oviposición' en este bosque durante el periodo de estudio, sino que es más bien una especie facultativa que explota las plantas no nativas para su beneficio reproductivo.

Palabras clave: biología de la conservación, especies invasoras, maladaptación, selección de sitio de anidación, trampa ecológica

INTRODUCTION

Humans are driving changes to ecosystems and the biosphere (e.g., habitat loss and fragmentation, spread of exotic species, and climate change) at a global scale and historically rapid pace (Meyerson and Mooney 2007, Vitousek et al. 2008, Hobbs et al. 2009). One consequence of rapid anthropogenically driven change is the introduction of new species and the reshuffling of existing species assemblages to create novel ecosystems and communities (Hobbs et al. 2009). Some extant species respond to ecological novelty with apparently adaptive behaviors, allowing them to thrive, while other species exhibit maladaptive responses to novel species interactions or

stimuli (Sih et al. 2011, Candolin and Wong 2012, Robertson et al. 2013).

An increasingly common consequence of ecological novelty is the creation of evolutionary traps (Dwernychuk and Boag 1972, Robertson et al. 2013). To make decisions, organisms commonly use environmental cues to assess current or future conditions. However, rapid environmental change can disrupt the historical relationship between the cue(s) that organisms respond to and the fitness consequences of that response (Levins 1968, Schlaepfer et al. 2005, Robertson and Hutto 2006, Sih et al. 2011). An evolutionary trap occurs when a resource is preferentially exploited by a species, but leads to a worse fitness outcome than less preferred alternatives (Schlaepfer et al. 2002, Robertson and Hutto 2006). Many examples of evolutionary traps undermining an array of behaviors (e.g., habitat selection ['ecological traps'], mate selection, and navigation) have been described, and traps now appear to be more common than was previously assumed (Robertson et al. 2013). Modeling approaches universally agree that, unless individuals learn or populations evolve, traps accelerate the decline of affected populations (Delibes et al. 2001, Donovan and Thompson 2001, Kokko and Sutherland 2001, Fletcher et al. 2012). Because the demographic effects of traps are often not isolated, but work in concert with other sources of population decline, evolutionary traps are emerging as an important conservation concern (Schlaepfer et al. 2002, Battin 2004, Robertson et al. 2013).

Exotic species have recently emerged as the most common cause of evolutionary traps, affecting a diversity of taxa and triggering traps within a broad array of behavioral contexts (Robertson et al. 2013). For birds, evolutionary traps can be predators that increase typical nest predation rates in preferred nesting sites (Igual et al. 2007), dominant plants that are good for concealing nests but support a reduced food supply (Lloyd and Martin 2005), or plants that provide a preferred food source but that are associated with reduced nest success (Rodewald et al. 2011). Indeed, ornithologists have been concerned for more than a decade that exotic plants might act as evolutionary traps for songbirds by acting as attractive, but dangerous, substrates in which to place nests (Schmidt and Whelan 1999, Chalfoun and Schmidt 2012).

Several studies have demonstrated that the reproductive success of songbirds is lower when nests are placed in exotic plants rather than in native nesting substrates (Schmidt and Whelan 1999, Borgmann and Rodewald 2004, Rodewald et al. 2010, 2011), which is consistent with the role of exotic plants as evolutionary traps. Yet no study has been explicitly designed to test whether nesting birds actually prefer exotic nest substrates over available native options, a critical criterion in determining the existence of a trap (Robertson and Hutto 2006, Robertson et al. 2013). Confirming that birds exhibit a preference for exotic nesting substrates or do not discriminate between native and exotic substrates is critical to determining whether birds are adaptively selecting nest sites, or are unaware of the fitness costs associated with exotic sites and thus are caught in an evolutionary trap.

The goal of this study was to evaluate the hypothesis that exotic plants are evolutionary traps for songbirds by acting as highly attractive nest sites or nest patches that lead to relatively worse reproductive outcomes than native options. We chose to test this hypothesis within a temperate deciduous forest in the northeastern United States, where in previous studies other bird species were shown to have reduced reproductive success when they placed their nests in exotic plants (Borgmann and Rodewald 2004, Rodewald et al. 2010, 2011, Chalfoun and Schmidt 2012). Researchers in these earlier studies, however, did not quantify the relative preference that birds had for placing their nests in native vs. exotic plants. We examined preferences for 3 plant species that were associated with reduced nest success in previous work: (1) Multiflora rose (*Rosa multiflora*; hereafter, 'rose'), (2) Amur honeysuckle (*Lonicera maackii*; hereafter,'honeysuckle'), and (3) Japanese barberry (*Berberis thunbergii*; hereafter, 'barberry'). We studied a population of color-banded Veeries (*Catharus fuscescens*), a common ground- and shrub-nesting songbird of this ecosystem known to use the above plant species as nest substrates (Schmidt 2003, Heckscher 2004, Heckscher et al. 2014). To support our hypothesis it would be necessary to show that: (1) Veeries prefer to place their nests in one or more exotic plant species relative to available native substrates (defined as a 'severe trap'), or place nests in native and exotic substrates in direct proportion to their availability indicating a lack of preference (an 'equal-preference trap'), and (2) reproductive success associated with nests placed in exotic species is lower than that for nests located in native plants (Robertson and Hutto 2006, Robertson et al. 2013).

METHODS

Study Site and Species

Our study was conducted from May 25 to August 15, 2013, in an 810 ha plot of eastern temperate deciduous forest located on the property of the Cary Institute of Ecosystem Studies in Dutchess County, southeastern New York State, USA. Forest at the site is relatively unfragmented and characterized by intermediate mesic, boggy areas with mainly secondary growth tree architecture. The most abundant invasive exotic shrubs throughout the study site are honeysuckle, barberry, and rose.

The Veery is an insectivorous, area-sensitive, forest-inhabiting Neotropical migrant bird species whose population has declined >60% since 1966 (Bevier et al.

2005, Sauer et al. 2014). Veeries typically conceal their nests in small shrubs or forbs (Schmidt 2003, Bevier et al. 2005), are common throughout the study site, and are known nest in rose, honeysuckle, and barberry (Schmidt 2003, Heckscher 2004, Heckscher et al. 2014). Territories are typically 0.1–2.0 ha in size (Bertin 1975; $\bar{x} = 1.8$ ha at our site, K. Schmidt personal observation) and are aggressively defended (Holmes and Robinson 1988). Females begin building nests in early May and egg laying begins in mid-May and extends through June (Bevier et al. 2005). Veeries typically produce only a single brood per year, but double-brooding is known to occur (Bevier et al. 2005). Eggs and nestlings are susceptible to avian predators, including Blue Jays (*Cyanocitta cristata*), American Crows (*Corvus brachyrhynchos*), and *Accipiter* spp., and mammalian predators, such as gray squirrels (*Sciurus carolinensis)*, eastern chipmunks (*Tamias striatus)*, white-footed mice (*Peromyscus leucopus*), raccoons (*Procyon lotor*), and weasels (*Mustela* spp.; Bevier et al. 2005).

Nest Substrate and Patch-Site Selection

Structural features of vegetation at nest sites were characterized to enable comparisons between (a) successful and failed nests, (b) nests placed in exotic vs. native plant species, and (c) vegetation structure in patches surrounding nest sites and in randomly located patches within territories. We measured floristic and structural habitat components potentially important to Veeries at 3 spatial scales: nest, nest substrate plant, and a plot centered on the nest with a 5-m radius.

We measured nest height and nest cup visibility as possible variables that could explain the probability of nest survival, because nest placement and visibility may differentially predispose some nests to being accessed or detected by nest predators (Martin 1998). Nest cup visibility was assessed from a height of 1 m from the 4 cardinal directions at a distance of 1 m, 2 m, and 5 m. Visibility was considered positive if any portion of the nest bowl was visible. We used these data to compile an index of visibility in which a nest could score 0–12 (0 = completely hidden; 12 = completely exposed) based on its bowl visibility at each of the 12 locations.

Disproportionate use of a resource relative to its availability is an indication of preference for that resource (Robertson and Hutto 2006). We compared vegetation characteristics at and surrounding the nest site with those of a paired randomly located plant within a surrounding patch of 5 m radius within 40 m of the nest site, but most likely within the territory of that pair of birds. We located these unused but available sites within occupied territories by generating a random number for distance (10–40 m) and degree (0–360°) from the nest. This range of distances from the nest placed the random plot within a radius of 80 m, which corresponded to a typical Veery territory size of 2.0 ha (K. Schmidt personal observation). At each random point we identified the nearest fallen limb or forb stem of a species in which Veery are known to have nested at this study site during the past 10 years (K. Schmidt personal observation).

The random point formed the center of the paired vegetation plot of 5 m radius that we compared with a plot of the same radius centered on the nest site. Within each nest-centered and random-point vegetation patch we assessed: (1) the density of forb and shrub stems of each nesting substrate, and (2) the vertical density of vegetation. We used the former as an indication of the relative abundance of different plant species that may have served as nesting substrates, while we used the latter to test the hypothesis that birds were placing nests in sites with high vegetation density, regardless of the site's species composition. We conducted stem counts only for the 3 exotic (barberry, honeysuckle, and rose) and 9 native plant species (American beech [*Fagus grandifolia*], ironwood [*Carpinus caroliniana*], witch hazel [*Hamamelis virginiana*], lowbush blueberry [*Vaccinium angustifolium*], mapleleaf viburnum [*Viburnum acerifolium*], cinnamon fern [*Osmundastrum cinnamomeum*], grass tussocks, blackberry [*Rubus* spp.], and fallen oak [*Quercus* spp.] limbs) in which Veeries are known to locate nests in our study site (K. Schmidt personal observation). We estimated vertical density of vegetation in 5-m radius plots as the percentage of a portion of a wooden pole visible from 5 m away from the nest at 1 m high from all 4 cardinal directions. We vertically oriented a 2-m long stick directly next to the nest and determined the percentage of the stick visible in 4 height categories: 0–10 cm, 10–50 cm, 50–100 cm, and 100–200 cm. Vegetation data were collected within a week after the fate of the nest was determined.

Nest Location and Monitoring

Four full-time technicians monitored all Veery nesting attempts using standard techniques (Ralph et al. 1993). We searched for nests beginning May 25, when males begin defending territories and females begin building nests and laying eggs (Bevier et al. 2005). A large percentage of Veeries in the study area is uniquely color-banded, facilitating accurate association of nests with individual pairs. Upon locating a nest, we placed a piece of flagging tape on vegetation at eye level >10 m from the nest in order to facilitate easier relocation of the nest. We monitored nests by visiting them every 1–4 days to verify that the nest was still active or to determine that the nest had failed. We concluded that a nest had failed if eggs or young were found in the nest cold and dead, or if <10-day-old nestlings were missing from the nest and fledglings were not seen in the area. We determined whether nestlings had fledged during the final nest visit by

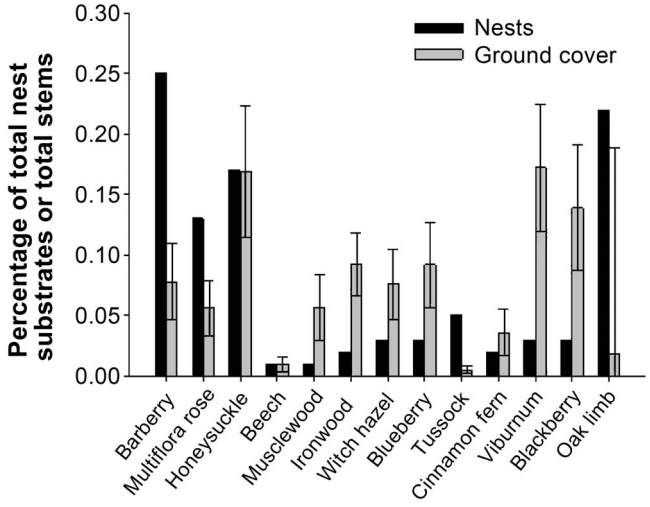

FIGURE 1. Selection of various plant species by Veeries as nest substrates compared with their relative stem density throughout the Cary Institute study area, New York, USA, 2013. Black bars indicate the percentage of the 84 nests located during the study placed in each plant species. Gray bars indicate the mean percentage (± 95% CI) of the total emergent stems in random 5-m radius sampling plots located within Veery territories.

observing fledglings, parental feeding on or after fledging dates, or identification of nestling begging calls, and by identifying strong antipredator aggression in response to our 'pishing' near the nest site. Nests close to their fledging date for which we could not locate parents or fledglings for 3 additional checks were given the fate "unknown" and excluded from all analyses.

Statistical Analysis

We used general linear models with unconditional bootstrapped errors to make comparisons of nest characteristics among vertical strata, between successful and failed nests, and between nests placed in native and exotic substrates. We estimated daily nest survival (the probability that a nest survives a given day) and tested hypotheses about the causes of variation in daily nest survival using the logistic exposure method of Shaffer (2004). We used a multimodel inference approach to determine the relative importance of 3 environmental variables in explaining variation in daily nest survival probability of Veery nests: (1) nest substrate (native vs. exotic), (2) vegetation density in 4 vertical strata, and (3) nest cup visibility. In a first analysis, we examined variation in nest success among 3 exotic substrates individually and all native substrates combined. In a second analysis, we combined nests in all nonnative plants into a single category.

First, all independent variables were entered into a full generalized linear model. Next, all possible subsets of the full model were analyzed using the multimodel inference package 'MuMin' in R version 2.11.1 (R Development Core Team 2009). We used this package to estimate model coefficients and bias-corrected Akaike's Information Criterion (AIC_c) values. Next, differences between the AIC_c values of the best model and the other candidate models (ΔAIC_c) were used to calculate Akaike weights (w_i) for each model. Weights of ranked models were then summed to construct a 90% confidence set of candidate models, after which Akaike weights were recalculated for each model in the 90% confidence set and used to calculate model-averaged parameter estimates and summed variable weights for each variable in the global model. Finally, Akaike weights for classes of variables were summed to assess the relative importance of different nest site characteristics.

RESULTS

We located 84 Veery nests. The most commonly used nest substrates were barberry (25%), fallen oak limbs (22%), honeysuckle (17%), rose (13%), grass tussock (5%), witch hazel (3%), and other (15%). Nonnative plant species accounted for more than half (55%) of nesting substrates. Comparisons among the percent stem composition of these substrates throughout the study area and their relative use suggested that Veeries generally avoided most native plants as nest substrates, preferring instead to place nests in barberry and rose (Figure 1). Fallen oak limbs were also used disproportionately to their availability, while there was no apparent preference for, or avoidance of, honeysuckle (Figure 1).

Veery nests placed in exotic plants were within 5-m radius habitat patches containing a larger fraction of exotic vegetation than nests placed in native plants, and the visual exposure of nests placed in exotic plants was lower (Table 1). We found fewer native stems within the 5-m patch surrounding nest sites compared with the random patches (nest patch vs. random patch: $\bar{x} = -5.0\%$; bootstrapped 95% CI: −8.5, −2.0). Yet, stem counts of none of the 3 individual nonnative species were greater at nest sites (all 95% CIs overlapped 0.0), indicating that Veeries were not exhibiting a strong preference for locating nests in patches of any focal nonnative plant species. Stem counts were higher in nest patches than in random plots across all vertical strata classes, and were highest in lower vertical strata (nest vs. random: $F_{1,648} = 130.7$, $P < 0.001$; height: $F_{3,648} = 360.6$, $P < 0.001$; interaction: $F_{3,648} = 5.3$, $P = 0.001$; Figure 2).

Daily nest survival probability was poorly explained by all explanatory variables, and there were no important differences among nonnative nest substrate species in their ability to explain variation in nest survival probability (Table 2A). Combining nests from all exotic substrates into a single 'exotic' category did improve the explanatory power of associated models, but power was still low, with relatively weak support across the entire model set ($w_i =$

TABLE 1. Comparisons of structural features of vegetation at Veery nest sites comparing: (a) successful and failed nests, and (b) nests placed in exotic vs. native plant species within the Cary Institute study area, New York, USA, 2013. The fraction of total vegetative stems surrounding nests that was composed of exotic plant species was higher for nests placed in native plants, but did not differ between successful nests (those that ultimately fledged >1 nestling) and failed nests. Visibility of nest bowls (as measured by a nest visibility index) was higher for nests placed in exotic plants, but the visibility of successful and failed nests did not differ. Values represent means ± unconditional SE and output of independent-samples *t*-tests. Significant *P*-values are highlighted in bold font.

	Nest vegetation substrate				Ultimate nest outcome			
	Native	Exotic	t_{79}	*P*	Successful	Failed	t_{59}	*P*
Percent exotic vegetation (5-m radius)	10.2 (3.9)	64.1 (3.7)	9.83	**<0.001**	56.6 (5.3)	65.5 (3.4)	1.63	0.10
Nest visibility index (1–12)	6.5 (0.5)	4.6 (0.4)	3.05	**0.03**	5.5 (0.6)	5.1 (0.5)	0.58	0.56

0.24; Table 2B). The best model in both analyses was the intercept-only model (species-specific: $w_i = 0.16$; native vs. exotic: $w_i = 0.11$) and the global models had very low weight ($w_i < 0.0001$). The variable weight (w_i) of the best-supported parameter from either analysis (percent exotic plant stems; Table 2B) was 0.31, indicating that this variable was found in only 31% of the best models explaining nest survival probability. Hypothesis tests of the importance of individual variables in explaining nest survival were significant only for the intercept and only in the species-specific multimodel inference analysis. Collectively, vegetation variables were poor predictors of Veery nest survival probability.

DISCUSSION

Evolutionary traps have the potential to undermine evolved behavioral algorithms where environments change more rapidly than populations can evolve or organisms can behaviorally adapt to novelty (Fletcher et al. 2012). We provide the first test of the hypothesis that birds prefer to nest in nonnative plant species where their reproductive success is lower than in native plants. Veeries in our study

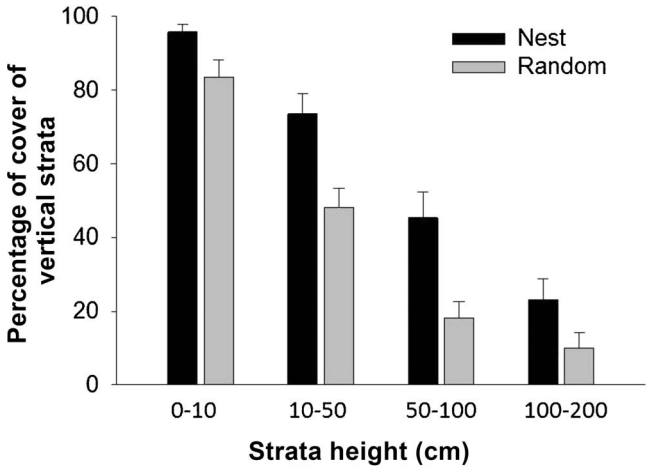

FIGURE 2. Vertical density of vegetation within various height strata surrounding Veery nest sites and at randomly located points in the Cary Institute study area, New York, USA, 2013. Vegetation surrounding nest sites was denser than that around randomly located points within Veery territories at all 4 vertical strata sampled. Vertical density was measured as the mean percentage of a portion of a wooden pole visible from 4 directions at 1 m high at a distance of 5 m. Bars show means with 95% confidence intervals.

TABLE 2. Parameter estimates (β ± unconditional SE) from the 90% confidence set of models predicting Veery daily nest survival probability as a function of nest concealment and environmental variables. Variable weights ($0 \leq w_i \leq 1$) quantify relative support for each variable across the entire set of models, which contained all possible combinations of predictors. Variable weights were obtained by summing w_i for all models in the set that included a given variable; weights approximate the likelihood that a given variable will be included in the final model. The model-selection procedure was completed using (**A**) a nest substrate variable that attributed nests to native plants vs. the 3 species of nonnative plant substrates, and (**B**) a nest substrate variable in which all nonnative nest substrates were grouped. Significance codes for likelihood ratio χ^2 critical values are: * $0.01 \leq P \geq 0.05$; ** $0.001 \leq P > 0.01$; *** $P < 0.001$.

Parameter	β (SE)	w_i
A		
Intercept	2.75 (0.28) ***	1.00
Nest substrate [a]		0.00
Barberry	−0.19 (0.41)	
Honeysuckle	−0.08 (0.58)	
Rose	−0.52 (0.51)	
Percent exotic (5-m radius)	0.00 (0.02)	0.29
Vertical density		
0–10	0.01 (0.02)	0.22
10–50	0.00 (0.01)	0.20
50–100	0.01 (0.01)	0.26
100–200	−0.01 (0.01)	0.22
Cup visibility	0.06 (0.07)	0.30
B		
Intercept	2.71 (1.12)	1.00
Nest substrate [a]		
Nonnative	0.28 (0.38)	0.24
Percent exotic (5-m radius)	0.00 (0.02)	0.31
Vertical density		
0–10	0.01 (0.02)	0.20
10–50	0.00 (0.01)	0.18
50–100	0.01 (0.01)	0.25
100–200	−0.01 (0.01)	0.21
Cup visibility	0.06 (0.07)	0.28

[a] Native was the reference category.

preferred to locate their nests in nonnative plants in denser patches of vegetation dominated by nonnative plants, a pattern that was also observed for Veeries nesting in mixed-hardwood forests in Delaware, USA (Heckscher 2004). However, we found no evidence that these preferences were maladaptive, in that there was no difference in the daily survival probability of nests or productivity of nests placed in native vs. exotic plants or patches dominated by native vs. exotic vegetation. Our results indicate that an evolutionary trap in oviposition behavior (i.e. an 'oviposition trap') was not in operation in this forest system during the period of our study. Rather, our evidence indicated that Veeries were facultatively exploiting nonnative plants as equally suitable nest substrates as their native counterparts.

Spatial and temporal variation are important characteristics of most ecological systems, and the absence of an ecological trap during the single breeding season that we studied does not preclude the existence of a trap in other years. In our study system, ground-foraging predator density is largely determined by the yearly acorn mast, and can vary by 2 orders of magnitude (Schmidt and Ostfeld 2008). Veery nests in this forest are protected against some nest predation by thorny-branched barberry; however, this benefit is typically limited to years with an elevated abundance of ground-foraging predators (Schmidt et al. 2005), mesic locations that favor barberry, and drier seasons (Chalfoun and Schmidt 2012). Fallen oak limbs were a preferred nest substrate in our study and are used by Veeries elsewhere (Heckscher 2004, Heckscher et al. 2014). They typically represent $<1\%$ of Veery nest sites in our study area (K. Schmidt personal observation), but represented 50% of Veery nest sites in 2012 (K. Schmidt personal observation) and 25% in 2013 (this study). This was due to a highly unusual mid-October snowstorm in 2011 that brought down thousands of limbs across the study area. The still-attached, dried-brown oak leaves closely matched the dorsal color of adult Veeries and may have acted to camouflage incubating females nesting in fallen oak limbs. The changing availability of nest substrates across years suggests that the adaptive nature of substrate preference is context-dependent and may also be under selection to reduce predation risk of adult birds (Amat and Masero 2004, Refsnider and Janzen 2010), as much as for its ability to provide suitable microclimate and prevent visual detection by predators of eggs and nestlings. Moreover, because traps may only manifest after the nesting cycle by differentially reducing the survival of fledglings raised in areas containing preferred resources (Bartos Smith et al. 2012, Shipley et al. 2013), the lack of difference in nest survival and fledglings produced from nests in native vs. exotic vegetation is not irrefutable proof that adults nesting in exotic vegetation do not experience reduced fitness.

The density of white-tailed deer (*Odocoileus virginianus*) has increased dramatically in the northeastern United States over the last decade, shifting the species composition of understory vegetation (Russell et al. 2001, Côté et al. 2004) and sometimes favoring the invasion of exotic plant species (Augustine and Jordon 1998, Eschtruth and Battles 2009). Where native plants are differentially removed in favor of exotics, this has the potential to restrict nest-site options for native birds. Deer are well-controlled through hunting in our study system, and exclusion experiments have confirmed that deer have not altered the species richness, abundance, and composition in seed banks, nor the density or diversity of forest saplings (Levine et al. 2012).

Many bird species locate their nests in exotic plants. The reproductive outcome associated with this behavior, however, has varied considerably among studies. Some illustrate that nests placed in exotic plants experience higher predation rates than nests in native plants (Schmidt and Whelan 1999, Remeš 2003, Borgmann and Rodewald 2004, Schmidt et al. 2005), while others report similar rates of nest success for nests placed in exotic and native substrates (Maddox and Wiedenmann 2005, Schmidt et al. 2005, Stoleson and Finch 2001), and still others demonstrate higher nest success in native plants (Schlossberg and King 2010). This variation in outcomes could indicate that the ecological consequences of nest-site choice are associated with species-specific plant traits or the natural history of the nesting species or its predators. Veeries in our study generally preferred denser patches of vegetation, and it may be that native vegetation is generally sparser in structure. Such variation could also result from spatial and/or temporal heterogeneity in fitness benefits conferred by exotic nest substrates, such that fluctuating selection pressures make the advantage of particular substrates context-dependent and variable through time. Under such conditions we should expect the evolution of nest-site preferences that reflect large-scale and/or long-term optima (Clark and Shutler 1999, Garshelis 2000). That Veeries in this and other studies (Heckscher 2004, Schmidt et al. 2005) have been found to exhibit adaptive nest site preferences across years with significant variation in predator numbers (Schmidt and Ostfeld 2008) and availability of nest substrates (Schmidt et al. 2005, this study) suggests that they may have evolved equally complex behavioral algorithms based on environmental cues that indicate current or future conditions. We chose our study system because, at the time of this study and according to the published literature, the plant species we focused on represented those most likely to trigger an evolutionary trap in avian oviposition behavior. Yet, despite the lack of any evidence for maladaptive behavior in this study, it remains entirely possible that oviposition traps of

the type we investigated are, in fact, common in this system and others on annual or longer timescales.

Remeš (2003) demonstrated that Blackcaps (*Sylvia atricapilla*) preferentially settled in plantations of exotic black locust (*Robinia pseudoacacia*), yet experienced higher nest predation and lower nest success in this habitat compared with native mixed-species forest. While this scenario does describe an ecological trap for this species associated with a nonnative plant, the attraction of Blackcaps to exotic plantations may be associated with cues extrinsic to the value of locust trees as suitable oviposition sites (e.g., enhanced food availability), such that habitat preference is strongest at the patch scale and limits the subsequent ability of individuals to make adaptive oviposition site decisions (Hutto 1985). Consequently, Remeš (2003) did not test whether an 'oviposition trap' was in operation. Alternatively, birds may select territories based heavily on the availability of nests sites or their relative quality, which would mean that deceptively attractive nest sites could drive maladaptive habitat preferences. Because we did not compare vegetation characteristics within territories and in sites that that were unoccupied by Veeries, we make no inferences about whether a trap is occurring as a result of a preference for falsely attractive territories, but our results do exclude the possibility that subsequent nest-site selection is maladaptive.

Consideration of spatial and temporal variation within the context of evolutionary traps is critical to distinguishing truly maladaptive responses from successful long-term behavioral strategies that may result in periodically low fitness over shorter timescales. To date, however, no empirical or modeling study has attempted to understand under what conditions spatial and temporal heterogeneity in the reliability of environmental cues should create traps vs. select for individuals capable of making adaptive decisions, even under exceptional conditions. Our results support other studies in showing that Veeries are successfully able to identify fitness-relevant physiognomic attributes of nonnative vegetation and to exploit exotic plants as a resource, and so are not suffering reduced nest success associated with the current distribution and composition of nonnative vegetation.

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Ethics statement: This research was conducted in compliance with the Guidelines to the Use of Wild Birds in Research.

LITERATURE CITED

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