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Effects of invasive woody plants on avian nest site selection and nesting success in shrublands

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Abstract

Exotic, invasive plants are a growing conservation problem. Birds frequently use invasive plants as nest substrates, but effects of invasives on avian nesting success have been equivocal in past studies. In 2004 and 2005, we assessed effects of invasive woody plants on avian nest-site selection and nesting success in western Massachusetts shrublands. At the nest scale, we tested the effects of invasive versus native substrates on nesting success as well as differences among individual invasive species. At the patch scale, we tested effects of invasive prevalence on nesting success in natives and invasives. We found that, as a whole, shrubland birds preferred invasive substrates. Of two species sufficiently abundant for individual analysis, gray catbirds *Dumetella carolinensis* preferred invasive substrates, but chestnut-sided warblers *Dendroica pensylvanica* showed no preference for natives or invasives. At the nest scale, nests of gray catbirds placed in invasive substrates were more successful than those in natives. Chestnut-sided warblers and all species combined, however, had equal nest success in invasives and natives. We found no differences in nest success for nests in different species of invasive substrates or in invasive substrates with and without thorns. At the scale of the patch, nest success in invasive substrates increased with the prevalence of invasives on a site. Nest success in native plants did not change with invasive prevalence. We attribute this finding to the tendency for thickets of invasive plants to be larger on sites with more invasive cover. These findings illustrate the complex interaction of different factors that can determine how invasive plants affect avian nesting success. We conclude that control of invasive woody plants should be neutral for most shrubland birds.

Introduction

Invasive exotic plants are considered a major conservation threat to native ecosystems (Wilcove *et al*., 1998; Mack *et al*., 2000; Pimentel *et al*., 2000). For birds, though, research on the impacts of invasive plants on nesting has produced equivocal results. Many bird species readily nest in invasive plants, and some birds seem to prefer invasives over natives as nesting substrates (Whelan & Dilger, 1992; Heckscher, 2004). Effects of invasives on nest predation rates, however, have varied considerably among studies. In some cases, nests placed in invasive plants had higher predation rates than nests in native plants (Schmidt & Whelan, 1999; Remeš, 2003; Borgmann & Rodewald, 2004). Elsewhere, nest success was equal in invasive and native substrates (Stoleson & Finch, 2001; Maddox & Wiedenmann, 2005; Schmidt *et al*., 2005). Given the potential negative impacts of invasive plants, understanding their effects on birds has important implications for both avian conservation and management of invaded habitats.

Most past studies of the effects of nesting in invasive plants have taken place in forest understory invaded by exotic shrubs (Schmidt & Whelan, 1999; Borgmann & Rodewald, 2004; Schmidt *et al*., 2005). In contrast, effects of invasive plants on birds in shrublands have received little attention. Old fields, powerline rights-of-way, and other disturbed, early-successional habitats are frequently invaded by exotic woody plants (Meiners, Pickett & Cadenasso, 2002; King *et al*., 2009). Shrubland birds are declining throughout the eastern US, primarily because of habitat loss and reductions in logging and other types of forest disturbance (Dettmers, 2003; Schlossberg & King, 2007). Thus, understanding the impacts of invasive plants on shrublands is important for conservation. If invasive plants negatively impact shrubland birds, then controlling invasives should be emphasized in shrubland management.

Effects of invasive plants on avian nesting success will depend, in large part, on the extent to which birds choose to nest in invasive plants (Delibes, Gaona & Ferreras, 2001). An invasive shrub that reduces nest success but is rarely used

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by birds is of little concern. In contrast, a harmful invasive that is highly preferred as a nest substrate can create an ecological trap (Schlaepfer, Runge & Sherman, 2002). Past studies indicating apparent preferences of birds for invasive substrates have been conducted in areas with few suitable native substrates (Whelan & Dilger, 1995; Heckscher, 2004). Thus, whether birds prefer native or invasive substrates when given a choice is largely unknown.

Research on nest predation has shown that factors on several spatial scales can affect avian reproduction. Here, we focus on two scales that appear especially relevant for birds nesting in invasive plants. First, at the scale of the nest itself, characteristics of invasive substrates may influence nesting success (Martin, 1992, 1993). In some habitats, the growth form of invasive woody plants is distinct from that of native plants. In the north-eastern US, for instance, invasive shrubs often form dense, foliose clusters and large thickets, a growth form that is uncommon in native plants (Ehrenfeld, 1997; Richburg, Dibble & Patterson, 2000; Drake, Weltzin & Parr, 2003). Dense foliage around a nest can lead to decreased nest predation (Martin & Roper, 1988; Martin, 1992), though effects of foliage cover are far from consistent (Howlett & Stutchbury, 1996; Chalfoun & Martin, 2009). Additionally, many invasive woody plants used as nest substrates by birds are conspicuously thorny. Nest substrates with thorns may offer some protection against nest predators (Tryjanowski, Kuzniak & Diehl, 2000; Quader & Sodhi, 2006), though again the evidence is mixed (Mezquida & Marone, 2002; Borgmann & Rodewald, 2004). Thus, the presence or absence of thorns could explain some differences in nest success between native and invasive substrates (Schmidt & Whelan, 1999).

At the scale of entire patches (roughly 5–20 ha in our system), the effects of invasives on avian nesting success may be influenced by the prevalence of invasive plants in the nesting patch. Invasive cover could affect nest predation on this scale in three ways. First, invasives could alter nest-site partitioning (Borgmann & Rodewald, 2004). In native-dominated habitats, birds often partition nest sites among plant species so that the density of nests in any given substrate is relatively low and predators cannot easily form a search image for nests in any given substrate (Martin, 1988). Plant invasions may increase the homogeneity of potential nest substrates by replacing a diversity of native plants with a monoculture of invasives (Whelan & Dilger, 1995). As a result, nest-site partitioning will be reduced on invaded sites, and nest predation could increase (see Bowman & Harris, 1980; Borgmann & Rodewald, 2004). Second, plant invasions may alter the number of potential nest sites that predators have to search (Martin & Roper, 1988; Chalfoun & Martin, 2009). Accordingly, greater cover of invasives could decrease nest predation rates by forcing predators to search more potential sites for nests, making them more likely to give up their search. Third, as discussed above, invasive plants often form large, dense thickets. Greater invasive cover may be associated with longer time since invasion and, as a result, the growth of larger thickets that could physically prevent predators from accessing nests (see Holway, 1991; Burhans & Thompson, 1999).

To date, research has given the most support to the idea that invasives harm nest success by altering nest-site partitioning. In studies where invasive plants created a monoculture, nests placed in invasives experienced relatively high predation rates (Schmidt & Whelan, 1999; Remeš, 2003; Borgmann & Rodewald, 2004). By contrast, where invasive plants were less common, nests placed in invasive plants tended to survive at least as well as those in native plants (Stoleson & Finch, 2001; Borgmann & Rodewald, 2004; Schmidt *et al*., 2005).

Our research addressed four questions about the impacts of invasive woody plants on birds nesting in shrublands: (1) Do birds prefer to nest in native or invasive substrates? (2) Does nesting success differ between native and invasive substrates? (3) Does nesting success vary by species or defenses of invasive substrate? (4) How does the patch-level prevalence of invasive plants affect the relative success of nests in invasive and native substrates?

Materials and methods

Study area

We studied avian nesting success on eight state-owned wildlife openings in western Massachusetts (Table 1). The wildlife openings were old fields or former clearcuts maintained in an early-successional stage by mechanical treatment approximately every 10 years. Sites had extensive cover of shrubs, vines and saplings and variable cover of herbaceous vegetation and remnant mature trees. Total areas of wildlife openings ranged from 9 to 89 ha (mean = 38 ha), and our nest-monitoring plots averaged 11 ha in size. Wildlife openings were generally bordered by mature forest. Western Massachusetts is heavily forested and lacking in early-successional habitat, so wildlife openings are important breeding habitats for birds that nest in shrublands or forest openings (King *et al*., 2009).

We recorded six species of invasive, woody plants on our study sites: multiflora rose *Rosa multiflora*, Japanese barberry *Berberis thunbergii*, Japanese honeysuckle *Lonicera*

Table 1 Locations of western Massachusetts Wildlife Management Areas sampled in 2004–2005 and number of nests monitored on each site

Wildlife Management Area	Latitude	Longitude	Number of nests
Cass Meadows	42°36′N	72°14′W	19
Eugene Moran	42°31′N	72°3′W	19
Herm Covey	42°15′N	72°21′W	14
Hiram Fox	42°21′N	72°53′W	14
Poland Brook	42°29′N	72°45′W	24
Savoy Hill	42°34′N	72°7′W	23
Williamsburg	42°26′N	72°44′W	8
West Leyden	42°39′N	72°36′W	44

japonica, oriental bittersweet *Celastrus orbiculatus*, common buckthorn *Rhamnus cathartica* and autumn olive *Elaeagnus umbellata*. All six species are known to displace native plants and are considered noxious weeds in all or parts of their North American ranges (Ehrenfeld, 1999; Richburg *et al*., 2000; Drake *et al*., 2003). We located nests in all invasive species except buckthorn, which only occurred on two sites in relatively small amounts.

Field methods

We searched for above-ground nests of birds from mid-May through early August of 2004–2005 and monitored nests on ~3–4-day intervals until they fledged young or failed. To confirm success for nests that may have fledged young, we searched for fledglings or adults carrying food nearby. For each nest, we recorded nest substrate, substrate height, nest height and distance to the nearest forest edge.

We measured vegetation on three to five circular 0.79 ha plots on each study site. The centers of all plots were at least 200 m apart and 50 m from forest edges. We positioned plots to maximize coverage of each study area. On each plot, we used the point-intercept method to measure vegetation at 20 randomly located points (Mazzei, 2009). At each point, we recorded the vegetation height as well as the plant species making up the canopy or the ground substrate (rock, litter, etc.) if no vegetation was present. We used the same plots in both years but different random points each year.

Vegetation analysis

For each year of data, we summarized vegetation cover by averaging per cent cover of each plant species on each site. Because vegetation cover appeared to change little between years, we averaged across the 2 years to produce the final data for analysis. We recorded small numbers of nonnative apple trees *Malus domestica* at five sites with old orchards. We elected to include apples with native plants because apples are not invasive and rarely spread without human assistance. We did not locate any nests in apple trees.

Nest-site preferences

To determine nest-site preferences, we compared the number of nests in invasive plants with the availability of invasive plants. We conducted separate analyses for all bird species combined and for individual species with sample sizes of at least 20 nests, including at least five in invasive substrates. For all birds combined, we first restricted vegetation data to points within the range of substrate heights used by birds on each site. Then, within those substrate heights, we calculated the mean cover of invasive and native woody plants on each study site. If birds choose native and invasive substrates at random, then the proportion of nests in invasives should equal the proportion of invasives among possible substrates on the study plots. For each site, we used a binomial test to determine the probability that the number of nests in invasive plants differed from what was available on the site. To determine overall selectivity, we combined results from all eight sites using Rice's (1990) combined probability test.

For individual bird species, sample sizes were too small to compute a probability of selectivity on each site. Instead, for each species, we computed the mean cover of invasive plants across all eight sites, with the result weighted by the number of nests found on each site. This weighted mean should reflect overall availability of native and invasive nest substrates for birds in our sample. We used a binomial test to determine whether the overall proportion of nests in invasive plants differed from the weighted mean of invasive plant cover. As above, we restricted our vegetation dataset to the range of substrate heights used by each species in our sample.

Nesting success

For birds' nests, we determined exposure days and nest fates using the criteria in Manolis, Andersen & Cuthbert (2000). We were primarily interested in the effects of invasive plants on nest predation. Thus, we excluded nests that failed due to abandonment or nestling starvation ($n = 6$); in most such cases we were uncertain whether the nest was active after being found. Our analyses included only bird species that nested at least once in invasive woody plants. Including species that never nested in invasives could confound effects of bird species and substrate on nest success. We pooled nests across years for analysis.

We determined effects of invasive plants on avian nesting success using logistic-exposure models. These are generalized linear models with a modified logit link function that accounts for the time length between nest visits (Shaffer, 2004). We used these models to run three analyses of invasive effects on avian nesting success:

(1) *Invasive versus native substrates*. For this analysis, we simply compared nesting success between nests in native and invasive woody plants. Though we grouped all five invasive plants together for this analysis, all five species share the tendency to grow in dense clusters, high foliage density and production of copious soft mast. We analyzed data for all bird species combined as well as for individual species with sufficient sample sizes.

(2) *Invasive plant species and plant defenses*. To determine how individual species of invasive plants affect nesting success, we compared nesting success among substrates for nests in multiflora rose, Japanese honeysuckle, autumn olive and Japanese barberry. We found only two nests in oriental bittersweet, which was too few for analysis. We determined the effects of plant defenses on nest predation by comparing nest survival between invasive substrates with thorns (barberry, bittersweet and rose) and without (honeysuckle and olive). Autumn olive does have thorns at the tips of its branches, but these likely present little impediment to climbing animals. For these analyses, we only had sufficient samples to run models for all bird species combined.

(3) *Invasive prevalence at the patch scale*. We examined effects of patch-level cover of invasive woody plants on nesting success. Cover of invasive plants was highly

correlated with the proportion of nests placed in invasive substrates ($r_8 = 0.90$, $P = 0.003$). For this analysis, we grouped all invasive woody plants into one category. Because we were interested in the relative success of nests in native and invasive substrates, the relevant test statistic was the interaction between nesting substrate (native vs. invasive) and patch-level invasive prevalence.

Many factors besides nest substrate can affect avian nesting success, and controlling for these factors may be necessary to determine effects of invasives. Thus, we included distance to forest edge, nest height and date as covariates in all analyses (see Chandler, 2006; Chandler, King & DeStefano, 2009). We considered including a site effect to control for potential differences in nest predation rates by study area. In exploratory analyses, however, nest success was unaffected by study site, whether considered a fixed or a random effect, so we excluded site from our final analyses.

For each analysis, we used PROC GENMOD in SAS to run logistic-exposure models. Because none of our independent variables were correlated, and the number of parameters in each model was small, we simply ran the full model and used χ^2-tests to assess parameter significance. We tested the fit of each model using the Hosmer–Lemeshow goodness-of-fit test (Hosmer & Lemeshow, 2000).

Results

On our eight study sites, cover of invasive woody plants ranged from 1.4 to 50.4% (Table 2). Multiflora rose was the most prevalent invasive plant, followed by autumn olive and Japanese honeysuckle (Table 2). We analyzed data for 165 above-ground nests from 17 species (Tables 1 and 3). Overall, 43% ($n = 94$) of above-ground nests were placed in invasive woody plants; by contrast, invasive plants made up a mean of 32 ± 10% of woody plant cover. For all birds combined, nests were more likely to be in invasive plants than would be expected by chance (Rice's combined probability test, $P = 0.0003$). Two bird species had sufficient sample sizes for individual analysis. Gray catbirds *Dumetella carolinensis* preferred to nest in invasive woody plants over natives (binomial test: $P = 0.006$), but substrate choices of chestnut-sided warblers *Dendroica pensylvanica* did not differ from random (binomial test: $P = 0.41$).

Table 2 Cover of invasive plants, as a per cent of all woody cover, on Massachusetts wildlife openings, 2004–2005

Wildlife Management Area	Buckthorn	Barberry	Multiflora rose	Honeysuckle	Autumn olive	Bittersweet	Total invasive
Cass Meadows	11.8	0.0	0.0	0.0	0.0	0.0	11.8
Eugene Moran	0.9	0.5	0.0	0.0	0.0	0.0	1.4
Herm Covey	0.0	0.0	29.9	4.1	16.4	0.7	50.4
Hiram Fox	0.0	11.6	5.7	0.0	2.0	1.5	19.3
Poland Brook	0.0	3.1	4.2	16.7	8.3	0.0	32.3
Savoy Hill	0.0	0.0	0.0	13.4	3.0	0.0	16.4
Williamsburg	0.0	0.0	3.1	3.1	1.6	1.6	7.8
West Leyden	0.0	3.6	12.5	0.0	7.1	2.7	23.2
Mean ± SE	1.6 ± 1.5	2.3 ± 1.4	6.9 ± 3.6	4.7 ± 2.4	4.8 ± 2.0	0.8 ± 0.4	20.3 ± 5.4

Table 3 Sample sizes for avian nests in native and invasive substrates monitored on wildlife openings in western Massachusetts, 2004–2005

Species	Scientific name	Total exposure days	Nests in native plants	Nests in invasive plants
Alder flycatcher	*Empidonax alnorum*	73	5	1
American goldfinch	*Carduelis tristis*	30	1	1
American robin	*Turdus migratorius*	109.5	7	4
Black-billed cuckoo	*Coccyzus erythrophthalmus*	121	6	7
Blue jay	*Cyanocitta cristata*	75	4	1
Cedar waxwing	*Bombycilla cedrorum*	149.5	6	2
Chestnut-sided warbler	*Dendroica pensylvanica*	412.5	29	9
Eastern towhee	*Pipilo erythrophthalmus*	69	2	3
Field sparrow	*Spizella pusilla*	67	2	5
Gray catbird	*Dumetella carolinensis*	536	18	16
Indigo bunting	*Passerina cyanea*	131	4	7
Mourning dove	*Zenaida macroura*	25	1	1
Prairie warbler	*Dendroica discolor*	62	1	3
Red-eyed vireo	*Vireo olivaceus*	46	2	2
Song sparrow	*Melospiza melodia*	84.5	4	3
Veery	*Catharus fuscescens*	7	1	1
Yellow warbler	*Dendroica petechia*	114.5	1	5
All species combined		2112.5	94	71

Following are results from logistic-exposure analyses of nesting success:

(1) *Invasive versus native substrates*. For all bird species combined, the type of nesting substrate had no effect on nest success (Fig. 1, Table 4). For gray catbird, nest success was higher in invasive plants than in native plants (Fig. 1, Table 4). For chestnut-sided warbler, we found no support for any effects we tested (Table 4). Hosmer–Lemeshow tests indicated that all three models fit the data (Table 4).

(2) *Invasive plant species and plant defenses*. Nest success did not differ among nests placed in different species of invasive plants ($\chi^2_3 = 5.3$, $P = 0.15$, Fig. 2a). Similarly, nest success did not differ between invasive plants with and without thorns ($\chi^2_1 = 0.0$, $P = 0.98$, Fig. 2b).

(3) *Invasive prevalence at the patch scale*. We found a significant interaction between total invasive cover on a patch and nest substrate (Table 5). Nest success increased with invasive cover for nests in invasive substrates but was unaffected by invasive cover in native substrates (Fig. 3).

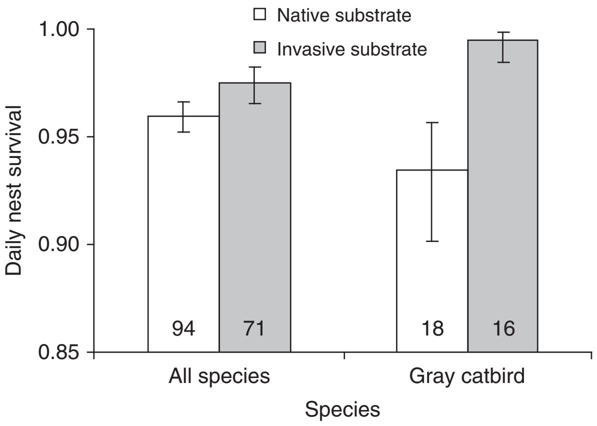

Figure 1 Effects of substrate on nest survival for all bird species and gray catbirds *Dumetella carolinensis*, based on logistic-exposure models. Error bars indicate 1 SE, and each bar is labeled with the sample size.

Discussion

Overall, birds in our study preferred invasive substrates over natives. Because we did not conduct fine-scale analysis of nest-site vegetation, we cannot know with certainty why birds exhibited this preference. We suspect that the dense foliage and thicket-forming habits of invasives made them attractive to nesting birds. Several past studies have shown that shrub-nesting birds prefer to nest in relatively dense vegetation or large thickets (Holway, 1991; Ricketts & Ritchison, 2000; Burhans *et al*., 2002; Heckscher, 2004). On our study sites, some native shrubs also form dense thickets, but these may be less attractive for nesting birds. Native spiraea (*Spiraea* spp.), for instance, formed large thickets on some sites, but spiraea thickets tend to be much lower in stature than those of invasives (D. King, pers. obs.). Additionally, native woody cover on our study sites was predominately sapling trees, which do not provide especially dense cover for nests. In contrast, clusters of multiflora rose and honeysuckle on our study sites had dense foliage and were several meters tall in some cases.

For gray catbirds the preference for invasive substrates was adaptive, as their nesting success was higher in invasives than in natives. For other bird species in our sample, however, choosing native or invasive substrates did not appear to have fitness-related consequences. In Connecticut shrublands, local abundances of catbirds were positively correlated with invasive cover, suggesting that catbirds actively select areas invaded by exotic shrubs (Mazzei, 2009). Similarly, Heckscher (2004) found that veeries *Catharus fuscescens* preferred nesting in areas with greater cover of invasive shrubs. Whether these preferences for nesting in invasives affect overall abundances of birds is not known. In a meta-analysis, Murray *et al*. (2007) found that abundances

Table 4 Parameter estimates for logistic-exposure models of effects of native versus invasive substrates

Species	Parameter	Estimate	SE	χ^2	*P*	Hosmer[a]
All species (*n*=154)	Substrate[b]	0.50	0.29	3.04	0.08	0.15
	Distance to edge	0.29	0.16	3.08	0.08	
	Date	**0.28**	**0.14**	**3.78**	**0.05**	
	Nest height	0.18	0.15	1.44	0.23	
Gray catbird (*n*=34)	**Substrate**	**2.62**	**1.01**	**6.67**	**0.01**	0.18
	Distance to edge	0.03	0.37	0.01	0.94	
	Date	**1.77**	**0.60**	**8.69**	**0.003**	
	Nest height	−0.43	0.44	0.96	0.33	
Chestnut-sided warbler (*n*=38)	Substrate	−0.91	0.84	1.18	0.28	0.10
	Distance to edge	0.28	0.49	0.32	0.57	
	Date	−0.44	0.37	1.40	0.24	
	Nest height	1.52	0.79	3.66	0.06	

[a] *P* value for the Hosmer–Lemeshow goodness-of-fit test for the full model.

[b] Effect of nesting in invasive plants.

Parameters significantly different from zero are in bold.

SE, standard error.

of birds were generally equal habitats with native or invasive plants.

Nest success was similar in all four species of invasive substrates that we tested. This was surprising, as the invasive plants we compared differ in structure, growth form and the presence of thorns. Differences among the invasives, however, may have been overshadowed by their similarity when compared with native substrates, the most common of which were spiraea, white pine *Pinus strobus* saplings, and a variety of deciduous saplings (D. King, unpubl. data). The presence of thorns in the substrate did not affect nest predation rates in our study. Past studies have found inconsistent effects of thorns on avian nesting success. Schmidt & Whelan (1999) found that nest success was higher in buckthorn (thorny) than honeysuckle (thornless). In contrast, Borgmann & Rodewald (2004) reported similar nest success in honeysuckle and multiflora rose (thorny). Effects of thorns on nest predation may depend on the specific predator, as birds may be less deterred by thorns than mammals or reptiles (Mezquida & Marone, 2002). More generally, we believe that the effects of individual invasive substrates on avian nest success will depend on the complex interaction of predator species, bird species and plant architecture (Borgmann & Rodewald, 2004). Thus, explaining why individual plant species do or do not affect avian nest success will likely require more in-depth research, including detailed description of nest location and identification of nest predators. For now, we conclude that no individual species of invasive plant on our study site had a noticeable impact on avian nesting success.

Our only significant finding at the nest scale was that gray catbirds had higher nest success in invasives than in natives. Estimated nesting success for catbirds over a 25-day nesting period was 71% in invasive plants versus 31% in natives.

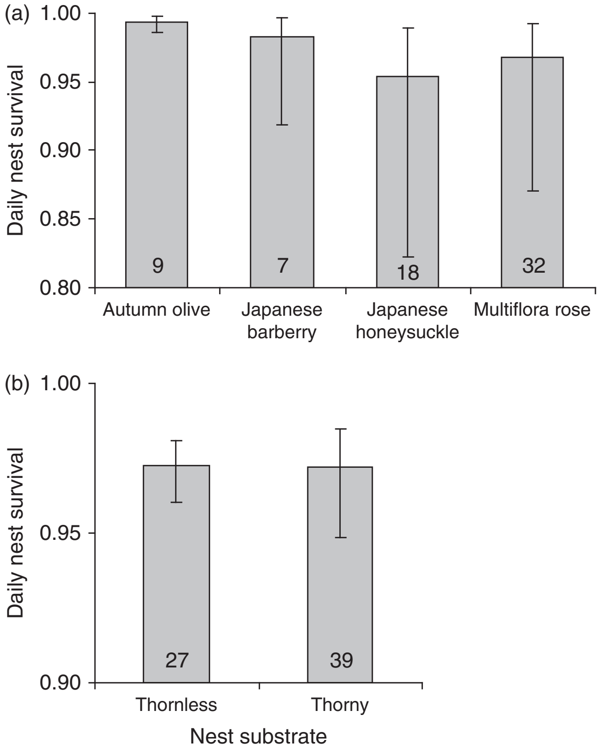

Figure 2 Effects of (a) species of invasive substrate and (b) presence of thorns on invasive substrates on nest survival for all bird species, based on logistic-exposure models. Error bars indicate 1 SE, and each bar is labeled with the sample size.

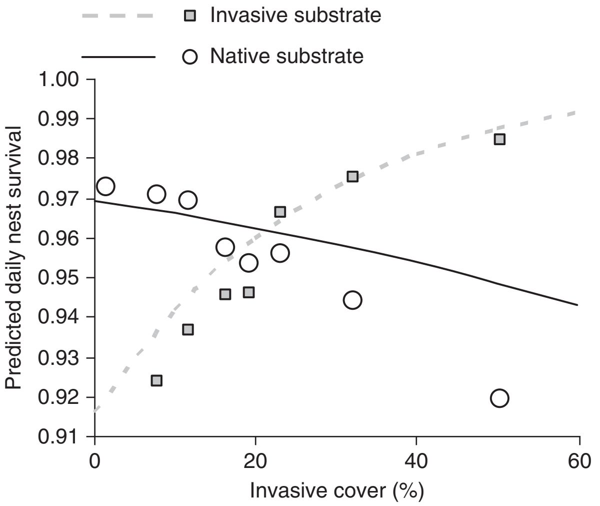

Figure 3 Effect of patch-level invasive cover on nest success of all bird species combined in native and invasive substrates. Data points are predicted nest survival on each site from a logistic-exposure model, and lines are regression curves estimated at the mid-point of the distributions of distance to edge, nest height and date in our dataset. Slope of the curve for native substrates was not significantly different from zero.

Table 5 Parameter estimates for logistic-exposure models of patch-level cover of invasive plants on avian nesting success

Parameter	Estimate	SE	χ^2	P	Hosmer
Invasive cover (native substrates)	−0.14	0.25	0.30	0.59	0.11
Invasive Cover (invasive substrates)	**0.50**	**0.21**	**5.72**	**0.02**	
Distance to edge	0.28	0.16	2.89	0.09	
Date	0.26	0.15	2.87	0.09	
Nest height	0.21	0.16	1.89	0.17	

Parameters significantly different from zero are in bold.
SE, standard error.

Why catbirds, unlike all other species, benefited from nesting in invasive plants is not known. We did not quantify cover around nests, but catbird nests are larger than those of most other species in our sample (Baicich & Harrison, 1997). Research suggests that larger nest size is correlated with increased nest predation (Møller, 1990). Thus, catbirds may have benefited disproportionately from the increased cover afforded by invasive over native substrates.

At the patch scale, nest success in invasives increased with invasive prevalence. Thus, our finding that overall nest success was equal in native and invasive substrates belies a more complex reality: nest success in invasives was similar to that in natives on sites with low invasive cover but greater on sites with high invasive cover. Nest predation in native substrates was unaffected by invasive prevalence, indicating that our results were not due to patch-level differences in predator abundances. This finding is contrary to the hypothesis that invasives decrease nest success by reducing nest-site partitioning. Rather, invasives either increased the number of nest sites to be searched by predators, or greater invasive cover deterred predation by physically blocking predators from reaching nests or restricting their movements on a site (Bowman & Harris, 1980; Holway, 1991). On our study, sites, multiflora rose, Japanese honeysuckle and autumn olive all form dense patches of vegetation that are virtually impenetrable to humans (D. King, pers. obs.). Invasive cover on our study sites was positively correlated with invasive height, which is an indicator of thicket size. In Missouri, Burhans & Thompson (1999) found that yellow-breasted chats had higher nest success in larger clusters of shrubs.

While we did not find negative impacts of invasive shrubs on avian nest success, our results do not imply that invasives are benign for shrublands as a whole. Multiflora rose, Japanese honeysuckle and other invasives can alter soils and displace native plants, which may necessitate control or eradication. Heckscher (2004) and Whelan & Dilger (1995) both suggest that removing invasive shrubs on their study sites would eliminate nesting habitat for shrub-nesting species such as veery. Every species in our study, however, nested in natives at least once. Thus, control of invasives followed by restoration of native shrub cover need not reduce habitat availability for shrubland birds. In addition, eradicating invasive shrubs in heavily invaded shrublands would not be expected to affect nest success for most birds because nest success did not differ between native and invasive substrates. Gray catbirds are an exception; however, catbird nest success in natives was 37%, which is typical for shrubland birds (Schlossberg & King, 2007). Still, research elsewhere has shown that removing invasive organisms can have a variety of unintended and unforeseen consequences (Zavaleta, Hobbs & Mooney, 2001). Our study did not examine effects of invasive plants on foraging efficiency or juvenile survival, both of which can affect reproductive success. Thus, our conclusions come with the caveat that effects of invasive control on shrubland birds need further research. In general, however, we expect that control of invasives in shrublands should not harm the nesting success of shrubland birds.

Acknowledgments

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References

Baicich, P.J. & Harrison, C.J.O. (1997). *A guide to the nests, eggs, and nestlings of North American birds*. New York: Academic Press.

Borgmann, K.L. & Rodewald, A.D. (2004). Nest predation in an urbanizing landscape: the role of exotic shrubs. *Ecol. Appl.* **14**, 1757–1765.

Bowman, G.B. & Harris, L.D. (1980). Effect of spatial heterogeneity on ground-nest depredation. *J. Wildl. Mgmt.* **44**, 806–813.

Burhans, D.E., Dearborn, D., Thompson, F.R. III & Faaborg, J. (2002). Factors affecting predation at songbird nests in old fields. *J. Wildl. Mgmt.* **66**, 240–249.

Burhans, D.E. & Thompson, F.R. III (1999). Habitat patch size and nesting success of yellow-breasted chats. *Wilson Bull.* **111**, 210–215.

Chalfoun, A.D. & Martin, T.E. (2009). Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses. *J. Anim. Ecol.* **78**, 497–503.

Chandler, R.B. (2006). *Early-successional bird abundance and nest success in managed shrublands on the White Mountain National Forest*. Masters thesis, University of Massachusetts, Dartmouth.

Chandler, R.B., King, D.I. & DeStefano, S. (2009). Scrub–shrub bird habitat associations at multiple spatial scales in beaver meadows in Massachusetts. *Auk* **126**, 186–197.

Delibes, M., Gaona, P. & Ferreras, P. (2001). Effects of an attractive sink leading into maladaptive habitat selection. *Am. Nat.* **158**, 277–285.

Dettmers, R. (2003). Status and conservation of shrubland birds in the northeastern US. *For. Ecol. Mgmt.* **185**, 81–93.

Drake, S.J., Weltzin, J.F. & Parr, P.D. (2003). Assessment of non-native invasive plant species on the United States Department of Energy Oak Ridge National Environmental Research Park. *Castanea* **68**, 15–30.

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

Ehrenfeld, J.G. (1999). Structure and dynamics of populations of Japanese barberry (*Berberis thunbergii* DC.) in deciduous forests of New Jersey. *Biol. Invasions* **1**, 203–213.

Heckscher, C.M. (2004). Veery nest sites in a Mid-Atlantic Piedmont forest: vegetative physiognomy and use of alien shrubs. *Am. Midl. Nat.* **151**, 326–337.

Holway, D.A. (1991). Nest-site selection and the importance of nest concealment in the black-throated blue warbler. *Condor* **93**, 575–581.

Hosmer, D.W.J. & Lemeshow, S. (2000). *Applied logistic regression*. New York: John Wiley & Sons Inc.

Howlett, J.S. & Stutchbury, B.J. (1996). Nest concealment and predation in hooded warblers: experimental removal of nest cover. *Auk* **113**, 1–9.

King, D.I., Chandler, R.B., Schlossberg, S. & Chandler, C.C. (2009). Habitat use and nest success of scrub–shrub birds in wildlife and silvicultural openings in western Massachusetts, U.S.A. *For. Ecol. Mgmt*. **257**, 421–426.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl*. **10**, 689–710.

Maddox, J.D. & Wiedenmann, R.N. (2005). Nesting of birds in wetlands containing purple loosestrife (*Lythrum salicaria*) and cattail (*Typha* spp.). *Nat. Areas J*. **25**, 369–373.

Manolis, J.C., Andersen, D.E. & Cuthbert, F.J. (2000). Uncertain nest fates in songbird studies and variation in Mayfield estimation. *Auk* **117**, 615–626.

Martin, T.E. (1988). On the advantage of being different: nest predation and the coexistence of bird species. *Proc. Natl. Acad. Sci. USA* **85**, 2196–2199.

Martin, T.E. (1992). Breeding productivity considerations: what are the appropriate habitat features for management? In *Ecology and conservation of neotropical migrant landbirds*: 455–473. Hagan, J.M. III & Johnston, D.W. (Eds). Washington: Smithsonian Institution Press.

Martin, T.E. (1993). Nest predation and nest sites: new perspectives on old patterns. *Bioscience* **43**, 523–532.

Martin, T.E. & Roper, J.J. (1988). Nest predation and nest-site selection of a western population of the hermit thrush. *Condor* **90**, 51–57.

Mazzei, B. (2009). *Monitoring birds and habitat in early-successional sites in Connecticut*. Masters thesis, University of Massachusetts, Dartmouth.

Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. (2002). Exotic plant invasions over 40 years of old field successions: community patterns and associations. *Ecography* **25**, 215–223.

Mezquida, E.T. & Marone, L. (2002). Microhabitat structure and avian nest predation risk in an open Argentinean woodland: an experimental study. *Acta Oecol*. **23**, 313–320.

Møller, A.P. (1990). Nest predation selects for small nest size in the blackbird. *Oikos* **57**, 237–240.

Murray, B.R., Dickman, C.R., Robson, T., Haythornthwaite, A., Cantlay, A.J., Dowsett, N. & Hills, N. (2007). Effects of exotic plants in native vegetation on species richness and abundance of birds and mammals. In *Pest or guest: the zoology of overabundance*: 216–221. Lunney, D., Eby, P., Hutchings, P. & Burgin, S. (Eds). Mosman: Royal Zoological Society of New South Wales.

Pimentel, D., Lach, L., Zuniga, R. & Morrison, D. (2000). Environmental and economic costs of nonindigenous species in the United States. *Bioscience* **50**, 53–65.

Quader, S. & Sodhi, N.S. (2006). What makes a good nest? Benefits of nest choice to female Baya weavers (*Ploceus philippinus*). *Auk* **123**, 475–486.

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

Rice, W.R. (1990). A consensus combined P-value test and the family-wide significance of component tests. *Biometrics* **46**, 303–308.

Richburg, J.A., Dibble, A.C. & Patterson, W.A. III (2000). Woody invasive species and their role in altering fire regimes of the northeast and mid-Atlantic states. In *Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species*: 104–111. Galley, K.E.M. & Wilson, T.P. (Eds). Tallahassee: Tall Timbers Research Station.

Ricketts, M.S. & Ritchison, G. (2000). Nesting success of yellow-breasted chats: effects of nest site and territory vegetation structure. *Wilson Bull*. **112**, 510–516.

Schlaepfer, M.A., Runge, M.C. & Sherman, P.W. (2002). Ecological and evolutionary traps. *Trends Ecol. Evol*. **17**, 474–480.

Schlossberg, S. & King, D.I. (2007). *Ecology and management of scrub–shrub birds in New England: a comprehensive review*. Report submitted to Natural Resources Conservation Service, Resource Inventory and Assessment Division, Beltsville.

Schmidt, K.A., Nelis, L.C., Briggs, N. & Ostfeld, R.S. (2005). Invasive shrubs and songbird nesting success: effects of climate variability and predator abundance. *Ecol. Appl*. **15**, 258–265.

Schmidt, K.A. & Whelan, C.J. (1999). Effects of exotic *Lonicera* and *Rhamnus* on songbird nest predation. *Conserv. Biol*. **13**, 1502–1506.

Shaffer, T.L. (2004). A unified approach to analyzing nest success. *Auk* **121**, 526–540.

Stoleson, S.H. & Finch, D.M. (2001). Breeding bird use of and nesting success in exotic Russian olive in New Mexico. *Wilson Bull*. **113**, 452–455.

Tryjanowski, P., Kuzniak, S. & Diehl, B. (2000). Does breeding performance of red-backed shrike *Lanius collurio* depend on nest site selection? *Ornis Fenn*. **77**, 137–141.

Whelan, C.J. & Dilger, M.L. (1992). Invasive, exotic shrubs: a paradox for natural area managers. *Nat. Areas J*. **12**, 109–110.

Whelan, C.J. & Dilger, M.L. (1995). Exotic, invasive shrubs: a paradox revisited. *Nat. Areas J*. **15**, 296.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998). Quantifying threats to imperiled species in the United States. *Bioscience* **48**, 607–615.

Zavaleta, E.S., Hobbs, R.J. & Mooney, H.A. (2001). Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol*. **16**, 454–459.