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Exotic shrubs as ephemeral ecological traps for nesting birds

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Abstract Certain exotic plants may increase risk of nest predation, and, in this way, may act as ecological traps. We hypothesized that the greater vulnerability to predation was a consequence of either (1) reduced nest height due to architectural differences among plant species or (2) seasonal changes in the distribution of nests among forest strata. To test this, we examined temporal variation in nest survival of 888 nests of Northern Cardinal (*Cardinalis cardinalis*) in native substrates and two exotic shrubs (*Lonicera maackii* and *Rosa multiflora*) in Ohio, USA, 2001–2006. We evaluated evidence for an ecological trap by monitoring the annual reproductive productivity of 245 breeding pairs of cardinals. Only nests in *Rosa* experienced relatively constant survival rates across the season, whereas probability of survival increased over the season for nests in other substrates. Interestingly, the relative vulnerability of nests in different substrates varied across the season. Most strikingly, nests in *Lonicera* in early spring showed the lowest survival rates but exceeded survival rates of nests in native substrates late in the season. Nest height failed to explain seasonal changes in nest survival, as only nests in native plants significantly increased in height as the season progressed. Rather, predation risk seemed to be a function of the proportion of nests within each substrate, as illustrated by the decreased predation in *Lonicera* as the relative proportion of nests in native substrates increased. The patterns of temporal variation in predation risk that we detected show that impacts of *Lonicera* are not a function of plant architecture alone and may be related to leaf phenology, changes in nest density, nest site location, and/or nest synchrony. Examination of the reproductive productivity of cardinals showed that pairs that made their first nest attempt in *Lonicera* fledged 20% fewer cardinal young than birds that began the season using other substrates. Thus, we suggest that exotic plants may represent an ephemeral ecological trap for certain nesting birds, where negative effects persist only during certain periods.

Keywords Birds · Ecological trap · Exotic · Nest · Predation · Productivity

Introduction

Although ecologists have long known that exotic invasive plants can profoundly impact ecosystem function and structure (Vitousek 1990), research has only recently demonstrated that exotic plants have the potential to alter predator–prey interactions. For example, exotic plants can reduce avian reproductive success in grassland (Scheiman et al. 2003; Lloyd and Martin 2005; Ortega et al. 2006) and forest habitats

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(Schmidt and Whelan 1999; Remes 2003; Borgmann and Rodewald 2004). Woody exotics in the forest understory may be especially likely to increase risk of nest predation to breeding birds (Schmidt and Whelan 1999; Borgmann and Rodewald 2004). In this way, ecologists have suggested that exotic shrubs may act as ecological traps by attracting understory-nesting birds to substrates that ultimately lead to lower nesting success.

Several potential mechanisms have been proposed to explain the increased risk of predation associated with certain exotic nesting substrates, including plant architecture, nest placement within a patch, nest placement within a substrate, and increased nest density (Schmidt and Whelan 1999; Remes 2003; Borgmann and Rodewald 2004). In addition, advanced leaf phenology of exotics may lead to increased predation if predators increase their foraging activity or efficiency in response to unusually high densities of nests early in the breeding season. Indeed, Remes (2003) observed that early leaf flush of introduced black locusts (*Robinia pseudoacacia*) led to an increase in density of Blackcaps (*Sylvia atricapilla*) in contrast to the surrounding bare native landscapes and, potentially, to elevated rates of nest predation. However, no studies have explicitly examined the extent to which risk associated with nesting in exotic shrubs varies temporally, nor specifically how nest height might contribute to increased vulnerability to nest predation.

In this study, we evaluated the extent to which exotic shrubs acted as ecological traps for understory-nesting birds and assessed the evidence for two general hypotheses that explain greater rates of nest predation in exotic than native substrates. One, we hypothesized that the greater vulnerability of nests placed in exotic substrates results from plant architecture, which lowers nest height and thereby improves access by predators. If this hypothesis were true, we predicted that nest height would be the primary driver of nest survival. Moreover, because plant architecture changes little across the season, nests in exotic substrates were predicted to experience consistently high predation across the season. Two, we hypothesized that the greater vulnerability to predation is a consequence of altered distribution of nests among nesting substrates in ways that either reduce diversity of nest sites or increase densities of nests within particular forest strata. We suspected that the early leaf flush exhibited by *Lonicera maackii* (Shustack et al. 2009) would promote nesting during a period when few alternative substrates are available. If this hypothesis were true, we further conjectured that the risk of nesting in exotic shrubs would vary temporally such that negative consequences were limited to the early spring. To evaluate the evidence for these hypotheses, we examined daily survival rates of nests of a common understory-nesting bird, the Northern Cardinal (*Cardinalis cardinalis*), in three nesting substrates (native plants, *Lonicera maackii*, and *Rosa multiflora*). Previous research in our study system shows that cardinals strongly select for dense understory vegetation, especially exotic shrubs, at both macro/patch- and nest-site scales (Leston and Rodewald 2006), despite experiencing higher rates of nest predation in exotics compared to native substrates (Borgmann and Rodewald 2004).

Methods

Fourteen mature riparian forest stands (104–277 m wide and ≥250 m long) were studied in central Ohio (ca. 40N00′, 83W00′). Sites were located along rivers approximately 20–40 m in width. Dominant trees at sites included eastern cottonwood (*Populus deltoides*), silver maple (*Acer saccharinum*), sugar maple (*Acer saccharum*), boxelder (*Acer negundo*), and hackberry (*Celtis occidentalis*; Leston and Rodewald 2006). Understory vegetation included seedlings and saplings of overstory trees as well as understory species such as dogwood (*Cornus* sp.), hawthorn (*Crataegus* sp.), spicebush (*Lindera benzoin*) and pawpaw (*Asimina triloba*). The most common invasive exotic shrubs were Amur honeysuckle (*Lonicera maackii*) and multiflora rose (*Rosa multiflora*), which dominate the understory community at most sites (Rodewald 2009; Borgmann and Rodewald 2005). Evidence from cameras deployed at nests and anecdotal observations indicate that sites support a wide variety of nest predators, including American Crow (*Corvus brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), Common Grackle (*Quiscalus quiscula*), Barred Owl (*Strix varia*), domestic cat (*Felis catus*), common raccoon (*Procyon lotor*), and Virginia opossum (*Didelphis virginiana*).

Nesting success

Nests were located and monitored from April through September 2001–2006. Nest-searching occurred within the framework of a larger project where we mapped territory locations of all breeding pairs. In this way, we could be confident that we located nests for most birds breeding at each site. Nests were monitored every 1–4 days through either successful completion or until failure. To avoid exposing nests to predators as a consequence of our visits, we observed nests from as far a distance as possible (often >10 m), for as brief a time as possible, and from different routes each time. If a predator was observed in the vicinity, we delayed checking the nest. At each nest visit, the status (active, not active) was determined by checking nest contents or observing parental behaviors (e.g., incubating, delivering food).

Over the 6 years of our study, 888 nests (3,463 nest–check intervals) of Northern Cardinals were classified as being placed in *Lonicera* spp. (primarily *L. maackii* with a few *L. tartarica*; 43.6% of nests), or *Rosa multiflora* (20.1%), or native substrates (36.2%), which included native shrubs, saplings, trees, vines (*Vitis* sp.), and dead debris within plants. Because we only located 33 additional nests in other species of exotic plants, they were not considered for analysis.

A logistic exposure model (Shaffer 2004) was used to estimate seasonal variation in daily nest survival rates for the various nesting substrates. The logistic exposure model accommodates variable time intervals between nest–checks intervals, does not make assumptions regarding when nest loss occurred, and can be applied using an information theoretic approach (Akaike's information criterion [AIC]) for multiple model analysis (Burnham and Anderson 1998). Using PROC GENMOD in SAS, we evaluated the following 19 a priori models to explain the variation we observed in daily nest survival rate (DSR) of cardinals based on combinations of julian date, year, substrate type (native, *Lonicera*, or *Rosa*), and nest height (Table 1). Each model was ranked relative to its deviate from the model with the lowest AIC score (i.e., the best model) by calculating differences in AIC scores (i.e., $\Delta\text{AIC} = 0$ indicated the highest ranked model). Models with $\Delta\text{AIC} < 2$ were considered to be equally plausible given the data. Akaike's weight (w) showed the weight of evidence for a particular model.

We more closely examined differences between early and late-season nests using a posteriori analysis of variance to examine seasonal changes in nest height, using nest as the replicate with substrate type, season (<julian date 168 vs. ≥julian date 168; see results for justification of categorization), and substrate by season interaction. We tested for changes in the relative proportion of nests located in the three substrate types over the season in an analysis of variance. In this last analysis, site was used as a replicate because the distribution of nests across substrates necessarily had to be calculated at a site or patch level.

Annual productivity

We estimated annual productivity by individually marking cardinals with a US Geological Survey aluminum band and a unique combination of color bands and then monitoring all nesting attempts throughout the season. For nests that successfully fledged young, numbers of young were determined by either counting the number of nestlings immediately prior to fledging and/or by observing parents and young for extended periods within 1–3 days of fledging. Individual cardinals at sites generally made 1–5 nesting attempts each breeding season. For each breeding pair, all nesting records over the season were compiled to determine the number of nesting attempts and the total number of young fledged over the season. We categorized pairs according to the substrate used for their first nest attempt (*Lonicera*, *Rosa*, or other). Associations between substrate and total number of cardinal young produced across the entire breeding season were analyzed in PROC GENMOD using a Poisson distribution.

Results

Of the 19 models representing alternate hypotheses to explain variation on daily nest survival rates, the highest ranked model ($\Delta\text{AIC} = 0$; $w_i = 0.72$) included julian date, substrate type, nest height, and a date × substrate interaction (Table 1). No alternate models were closely ranked ($\Delta\text{AIC} > 2$). Examination of parameter estimates and Type 3 tests of main effects showed that nest survival was a function of julian date ($\chi^2 = 17.12$, $P < 0.001$), substrate

Table 1 Results from information-theoretic approach to evaluate the relative performance of alternate models explaining daily nest survival of 888 Northern Cardinal nests in *Lonicera*, *Rosa*, or native substrates in central Ohio, 2001–2006

Model	Log likelihood	k	AIC	ΔAIC	w_i
Date + substrate + date × substrate + height[a]	−1,398.26	7	2,810.53	0.00	0.72
Date + height	−1,403.65	3	2,813.30	2.76	0.18
Date + substrate + height	−1,402.26	5	2,814.51	3.98	0.10
Date + substrate + date × substrate + year	−1,402.41	11	2,826.82	16.31	<0.01
Date + year	1,408.75	7	2,831.50	20.97	<0.01
Date + substrate + year	−1,406.81	9	2,831.63	21.11	<0.01
Date + substrate + date × substrate	−1,410.49	6	2,832.99	22.46	<0.01
Date	−1,415.83	2	2,835.66	25.12	0.00
Date + substrate	−1,414.45	4	2,836.89	26.36	0.00
Date + year + date × year	−1,406.60	12	2,837.20	26.69	0.00
Height + year	−1,412.02	7	2,838.03	27.50	0.00
Height + substrate	−1,418.04	4	2,844.08	33.54	0.00
Height	−1,421.17	2	2,846.33	35.80	0.00
Height + year + height × year	−1,411.29	12	2,846.57	36.06	0.00
Height + substrate + height × substrate	−1,417.46	6	2,846.92	36.39	0.00
Substrate + year	−1,421.18	8	2,858.36	47.84	0.00
Substrate + year + substrate × year	−1,415.69	18	2,867.37	56.90	0.00
Year	−1,427.97	6	2,867.93	57.40	0.00
Substrate	−1,431.21	3	2,868.42	57.89	0.00

[a] This top model included the following parameter estimates: intercept (2.6883 ± 0.578 SE), julian date (0.0004 + 0.004 SE), substrate (*Lonicera*: −1.738 ± 0.692 SE; Native: −0.901 ± 0.738 SE; *Rosa*: 0.000), julian × substrate (*Lonicera*: 0.013 ± 0.005 SE; Native: 0.008 ± 0.005 SE; *Rosa*: 0.000), and nest height (−0.0045 ± 0.026 SE)

($\chi^2 = 6.49$, $P = 0.039$), the date × substrate interaction ($\chi^2 = 7.99$, $P = 0.018$), but not specifically nest height ($\chi^2 = 0.03$, $P = 0.865$; see parameter estimates in Table 1).

Nest survival substantially increased throughout the season for native plants and *Lonicera*, but not for the nests located in *Rosa* (Fig. 1). Interestingly, daily survival rate for nests in *Lonicera* was lower than observed for the other two substrates early in the season but surpassed those in native substrates after approximately julian date 168, which corresponds roughly to early June.

A posteriori tests were performed to evaluate possible causes of this apparent shift in DSR using julian date as 168 to distinguish early from late season. We were particularly interested in how relative vulnerability of nests in *Lonicera* and native substrates changed with nest height and the distribution of nests among the three substrate types. Nest height was significantly greater for nests in native versus both exotic substrates (Full Model:

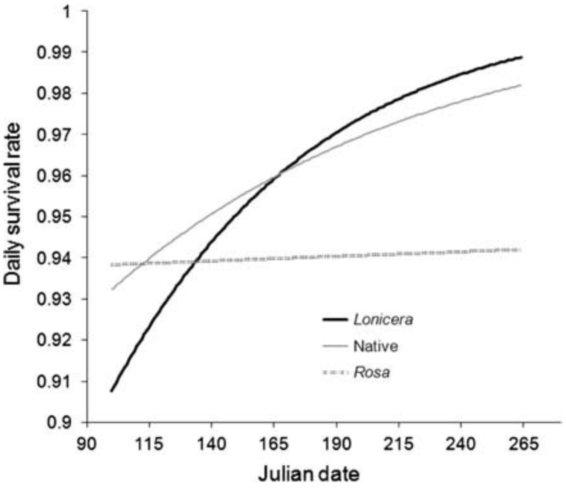

Fig. 1 Relationship between daily survival rate and julian date for Northern Cardinal nests located in three different substrate types, native ($n = 322$), *Lonicera* spp. ($n = 387$), and *Rosa multiflora* ($n = 179$) throughout the nesting season in central Ohio, 2001–2006. Graphical illustration is based on the top model identified in our information-theoretic approach

$F_{5,875} = 105.85$, $P < 0.0001$; $R^2 = 0.38$; Substrate: $F_{2,878} = 165.86$, $P < 0.001$), but this pattern was influenced by season as well (Fig. 2). Over the breeding season, nest height significantly increased (Season: $F_{1,879} = 25.76$, $P < 0.001$, Substrate × Season: $F_{2,878} = 12.10$, $P < 0.001$) by approximately 2 m for nests in native substrate but not substantially for nests in *Lonicera* and *Rosa*. Using each forest stand as a replicate, the proportion of nests located in native substrates increased by two times for native substrates between early and late season ($F_{1,27} = 13.05$, $P = 0.0013$), decreased by three times for *Rosa* ($F_{1,27} = 11.56$, $P = 0.0022$), but did not differ for nests in *Lonicera* ($F_{1,27} = 0.72$, $P = 0.4024$; Fig. 3). Thus, the overall proportion of nests in exotic substrates was much greater early than late in the season.

We estimated annual productivity for 245 pairs that made their initial nest attempt in either *Lonicera* ($n = 108$ pairs), *Rosa* ($n = 61$), or another ($n = 76$) substrate. Cardinal pairs that initiated the breeding season by nesting in *Lonicera* fledged 20% fewer young over the course of the season ($\chi^2 = 6.15$, $df = 2$, $P = 0.0462$). Pairs using *Lonicera* for a first nest fledged an average of 1.6 ± 0.15 SE young over the season compared to 2.03 ± 0.21 SE in *Rosa* and 2.01 ± 0.20 SE in other substrates.

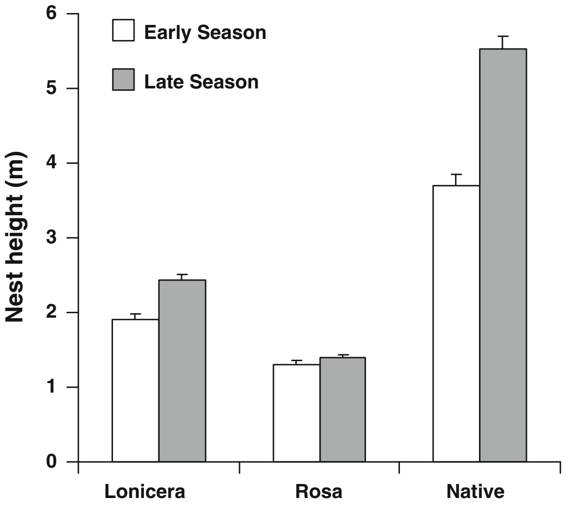

Fig. 2 Change in mean nest height (±SE) between early (julian date < 168) and late (julian date > 168) portions of the nesting season for nests in three substrates: native ($n = 322$), *Lonicera* spp. ($n = 387$), and *Rosa multiflora* ($n = 179$) in central Ohio, 2001–2006

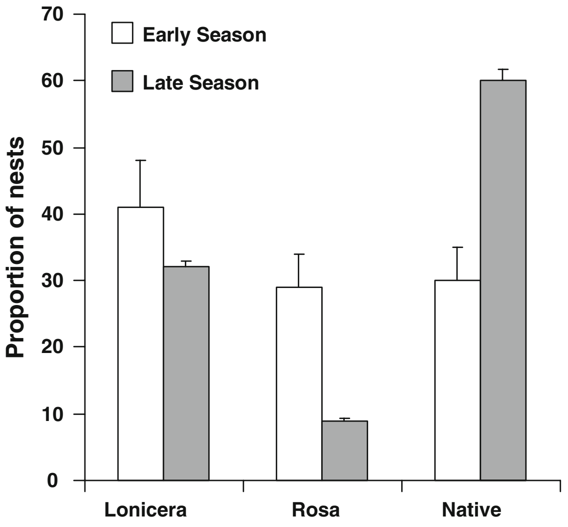

Fig. 3 Percent (±SE) of Northern Cardinal nests in each substrate for native ($n = 322$), *Lonicera* spp. ($n = 387$), and *Rosa multiflora* ($n = 179$) and contrasting between early (<168 julian date) and late (>168 julian date) periods of the nesting season for 14 study sites in central Ohio, 2001–2006

Discussion

Relative survival rates of nests in native and exotic substrates changed over the course of the breeding season and were lowest for nests in *Lonicera* early in the season. During this "early season", nests in *Lonicera* had extremely low daily survival rates of 91%, which translate to an abysmal 14% chance of survival over a 21-day nesting cycle. Nest survival rates in *Lonicera* improved dramatically later over the season and even exceeded survival rates in native substrates near the end of the breeding season. The higher risk of nest predation coupled with the fact that cardinals show strong preferences for nesting in *Lonicera* (Leston and Rodewald 2006) suggest that *Lonicera* may represent an ephemeral ecological trap. An ephemeral ecological trap differs from a more traditional trap because the negative consequences of the preference are restricted to particular time periods. Despite prior studies indicating that cardinal productivity is similar across our rural-to-urban gradient (Rodewald and Shustack 2008), we found choice of substrate was related to cardinal productivity within sites. Specifically, cardinal pairs that selected *Lonicera* as a substrate for their first nest attempt of the season fledged 20% fewer young over the course of the year than pairs that first nested in other substrates. We detected no reduced productivity for pairs selecting either *Rosa* or native substrates for their first attempts.

Our findings of temporally variable predation risk are consistent with past studies that show greater predation risk occurs early in the nesting season (Filliater et al. 1994; Dinsmore et al. 2002; Mahony et al. 2006). An increase in predation early in the season may be due to behavioral changes in predators or structural changes in the habitat (e.g., vegetation density and nest concealment). Our findings support a seasonal increase in DSR for nests located in *Lonicera* and native substrates, but not for those occurring in *Rosa*.

Although nest placement can directly impact nest survival (Martin and Roper 1988; Filliater et al. 1994), differences in nest height fail to explain why survival rates of nests in *Lonicera* changed so dramatically over the season in our study given that the marked increase in DSR of nests in *Lonicera* did not correspond to increases in nest height. Furthermore, temporal changes in DSR make it unlikely that plant architecture alone accounted for the increased vulnerability of nests in *Lonicera*, given that architecture did not dramatically change over the season.

The advanced phenology of *Lonicera* might have contributed to the pattern of depredation observed in this study by reducing nest site diversity or increasing synchrony of early nests, both of which can lead to greater nest densities within particular strata. Our previous work in this system confirms that bud break and leaf expansion are earlier in *Lonicera* than most other woody plants, especially overstory trees (Shustack et al. 2009). If birds choose to nest in substrates with early leaf flush, sites may have low nest-site diversity early in the season (e.g., vertical compression of nests into a narrower band of forest strata compared to later in the season). Reduced diversity of nest sites is known to increase risk of nest predation in other systems (Martin 1993a, b; Niemuth and Boyce 1995; Remes 2003). Indeed, nest predation was greatest for exotic substrates in the early spring when >70% of all nests were located in either *Lonicera* or *Rosa*, and DSR increased as more nests were placed in a variety of native substrates. Likewise, the increased synchrony of early nest attempts may affect vulnerability to predation, though results are mixed (Westneat 1992; Weatherhead and Sommerer 2001).

Our results show that previous studies that generalize about the overall impact of exotic shrubs on nesting birds (Schmidt and Whelan 1999; Borgmann and Rodewald 2004) may overlook important variation in predation risk within the season. Our findings also have some important implications for conservation and restoration efforts. If advanced leaf phenology guides, in part, the extent to which exotic substrates may act as ecological traps early in the nesting season, then ecologists may be able to predict which exotic plants may be most likely to negatively affect breeding birds, and consequently better target control or restoration effects. These findings also suggest that the negative consequences of exotic shrubs may be most acute for species nesting early in the breeding season, such as resident and short-distant migrant birds. For example, many long-distance migrants may arrive in breeding areas after leaf emergence is well underway in all strata, possibly buffering them from increased vulnerability to predation. Ultimately, effective conservation and requires that researchers move beyond documenting the impacts of exotic plant invasions, and identify underlying mechanisms that drive ecosystem and community-level consequences (Zavaleta et al. 2001).

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