

Behavioral consequences of plant invasion: an invasive plant alters rodent antipredator behavior

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Antipredator behavior is an important aspect of predator–prey dynamics and prey survival, and invasive species are becoming an increasing threat to ecosystems worldwide. Although these 2 concepts are frequently connected in terms of invasive predators and naïve prey, other effects of invasive species, such as the creation of novel habitats by invasive plants, may also have indirect effects on animal behavior and community dynamics. We used giving-up densities to examine foraging behavior of *Peromyscus leucopus* in forest habitats that were invaded or uninvaded by the exotic invasive shrub, *Lonicera maackii*, which forms a novel shrub layer in hickory–oak forests in Missouri. We experimentally manipulated the presence or absence of an artificial cover over foraging trays and predicted that rodents would have less of a preference for artificial cover in invaded sites with high densities of invasive shrub cover. We found that the invasive shrub decreased perceived predation risk, but this effect was contingent on other environmental correlates of predation risk (i.e., clear, moonlit nights) and foraging cost (i.e., warm temperatures). Our results demonstrate that invasive plants can change animal behavior, which may benefit the invasive species by causing apparent competition and promoting further invasion. Our results have implications for further behavioral changes that could affect multiple trophic levels and suggest that plant invasions can have cryptic, interactive effects on animal behavior, aside from their commonly studied effects on other plant species. **Key words:** antipredator behavior, foraging, giving-up densities, invasive species, rodent. [*Behav Ecol* 21:556–561 (2010)]

Antipredator behavior has important consequences for prey survival, prey population dynamics, and the stability of predator–prey interactions (Werner and Peacor 2003; Caro 2005; Preisser et al. 2005; Stankowich and Blumstein 2005), and it may also play an important role in biological invasions (Strauss et al. 2006; Sih et al., 2010). Investigations of antipredator behavior in biological invasions generally focus on interactions among nonnative predators and naïve prey (Snyder and Evans 2006; Sih et al., 2010). Less appreciated is that invasive plants may alter the antipredator behavior of consumers by creating novel habitats. Although invasive plants can dramatically change the structure and composition of the areas they invade (Vitousek 1986; Gordon 1998) and animals commonly exploit habitat structure to avoid their predators (Brown and Kotler 2004; Caro 2005; Stankowich and Blumstein 2005), few studies have examined how invasive plants may alter consumer antipredator behavior.

Understanding whether invasive plants alter consumer antipredator behavior is important because antipredator behavior can alter consumer distribution and abundance, ultimately affecting persistence. This is clearly evident in island systems, where introduced predators have strong effects on insular prey, presumably because island prey lack the appropriate antipredator behavior (e.g., Blumstein and Daniel 2005). However, antipredator behavior can be modified even when prey are adapted to predator presence if habitat is altered to change prey exposure (e.g., Loria et al. 2008). Moreover, changes in antipredator behavior can alter the dynamics of multiple trophic levels. For example, if invasive plants provide a low-risk refuge for native consumers, shifts in foraging behavior

caused by the provision of a refuge can alter the impact of consumers on plant populations (Holt and Kotler 1987; Connell 1990; Chanton and Bonsall 2000; Orrock et al. 2010). As plant invasions become more prominent as a component of global environmental change (Wilcove et al. 1998; Theoharides and Dukes 2007), their effects on varying trophic levels become more important to understand.

In this study, we examine whether the exotic woody shrub, *Lonicera maackii*, alters foraging by a ubiquitous rodent consumer, the white-footed mouse (*Peromyscus leucopus*) by creating a dense shrub layer that reduces perceived predation risk. Within deciduous forest woodlands, *P. leucopus* are common small mammals that experience predation pressure from avian and terrestrial predators (e.g., owls and foxes). Tree seeds may make up a considerable portion of their diet, which can also include insects and fruit (Lackey et al. 1985). Dynamics of *P. leucopus* may affect plant recruitment (e.g., Jones et al. 1998; McShea 2000), the abundance of forest insects (Ostfeld et al. 1996; Jones et al. 1998), and prevalence of tick-borne diseases that affect humans (Jones et al. 1998; Allan et al. 2003). *Peromyscus* spp. rodents, including *P. leucopus*, demonstrate perceived changes in predation risk in their environment by altering foraging in response to moonlight, weather, ground cover, canopy cover, and distance from vegetation (Manson and Stiles 1998; Orrock et al. 2004; Wolf and Batzli 2004; Orrock and Danielson 2009), and they have demonstrated a strong preference for shrubby covered habitats during foraging (Williams et al. 1992; Morris and Davidson 2000; Manson et al. 2001; Wolf and Batzli 2004; Meiners 2007; Matlack et al. 2008).

Lonicera maackii, a bush honeysuckle native to China, invades forests that previously lacked an understory shrub layer (Collier et al. 2002); invasion by *L. maackii* is associated with decreased growth and diversity of forest plant species due to direct competition (Hutchinson and Vankat 1997; Gould and

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Gorchov 2000; Collier et al. 2002; Gorchov and Trisel 2003; Miller and Gorchov 2004; Hartman and McCarthy 2007), as well as negative effects on reptiles and amphibians (McEvoy and Durtsche 2004) and birds (Schmidt and Whelan 1999; Bartuszevige and Gorchov 2006). Although it has been shown to affect other forest animals, the effect of invasive *L. maackii* on small mammals, and specifically antipredator behavior, remains unexamined. We assessed differences in *P. leucopus* giving-up densities between artificially covered and uncovered trays in invaded and uninvaded habitats. Giving-up densities were evaluated in light of other indirect cues of predation risk that are known to affect rodent foraging (e.g., moonlight; Brown and Kotler 2004; Orrock and Danielson 2004; Verdolin 2006). We expected rodents to perceive lower predation risk in areas invaded by high densities of *L. maackii* than in uninvaded areas. We predicted that rodents would exhibit a stronger preference for artificially covered trays over uncovered trays in uninvaded environments but would have less of a preference for artificial cover in invaded sites. Seed predators may show a preference for covered trays over uncovered trays in both environments, but the difference was expected to be smaller in areas invaded by *L. maackii* because the shrub will provide extra cover.

MATERIALS AND METHODS

Study sites

This study was conducted at August A. Busch Memorial Conservation Area in St Charles, MO (38°42'18N, 90°44'50W). We used 12 sites of mixed hickory–oak deciduous forest evenly distributed through the conservation area in this study; visual surveys indicated that 6 sites had very low *L. maackii* presence and that 6 sites were naturally invaded by high densities of *L. maackii*. Although uninvaded sites may have had very a small number of *L. maackii* shrubs present, they were dramatically different from invaded sites that contained a large number of mature individuals (88 times greater densities of *L. maackii*, see Results), so invaded and uninvaded treatments are considered distinct. Personal communication with park staff indicated that all sites were under the same management practices. Because all sites were used and managed similarly and we observed evidence of an advancing invasion front across the conservation area, we suspected that *L. maackii* was only absent from uninvaded sites because of its limited dispersal range, and it was likely to reach these sites in future years.

We created a 30 × 30-m plot centered within each of the 12 sites. The 12 sites were separated by a distance of at least 400 m. This distance is well beyond the size of the average home range of *P. leucopus* (1000 m², Lackey et al. 1985), that is, an area of approximately 30 × 30 m. As a result, it is very unlikely that mice foraged among multiple sites, which was also confirmed by our live-trapping data (see Results). Habitat data were collected at 12 subplots uniformly distributed in each plot. Data collected included 2 measures of light near the forest floor quantified as photosynthetic photon flux in μmol/m²/s as measured with an Apogee Quantum sensor held approximately 1 m above the ground and at ground level near midday under clear bright skies and leaf litter quantified as the number of leaves pierced by a metal dissecting probe stuck into the ground. Density of *L. maackii* was determined by counting *L. maackii* individuals greater than 1 m in height within a 1-m radius of the subplot center. Because we chose sites with either very few individuals or large mature stands, *L. maackii* individuals under 1 m in height were extremely rare within the study sites and were not expected to contribute significantly to the cover perceived by rodents.

Quantifying antipredator behavior

We quantified antipredator behavior using giving-up densities to measure perceived predation risk (Brown 1988; Morris and Davidson 2000; Brown and Kotler 2004; Orrock et al. 2004; Orrock and Danielson 2004; Wolf and Batzli 2004). This technique uses a known amount of seeds and sand placed in a foraging tray. As a foraging rodent depletes the seeds within a tray, diminishing returns are realized (Brown 1988; Morris and Davidson 2000). Eventually, the benefits of continued foraging are outweighed by the costs (Brown 1988). This threshold, called the giving-up density (Brown 1988), represents a quantitative measure of the costs of foraging (i.e., metabolic costs, missed-opportunity costs, and predation risk), because a rodent should stop foraging, or “give up” when the cost of foraging equals the diminishing rate of gain from foraging. To isolate the effect of predation risk, trays are presented in pairs, with one tray located under the cover of a protective object and an uncovered nearby tray. By pairing the trays, missed opportunities and metabolic costs are assumed to be the same within a pair. As such, the difference between covered and uncovered trays can be used to quantify predation risk experienced by rodents (e.g., Brown 1988; Morris and Davidson 2000; Orrock et al. 2004; Wolf and Batzli 2004).

On 16 October 2008, 2 foraging trays were placed approximately 1 m apart at each of the 12 study sites. Tray placement within the site was determined during a 3-week pilot study in which areas with potential for consistent foraging were identified, although foraging was never observed at some sites (see Results). Trays were translucent white plastic buckets of height 16 cm and diameter 18 cm with 2 5- × 5-cm holes cut opposite one another on the sides, approximately 3.5 cm from the bottom of the bucket to allow rodent access. Each tray was filled with 1 l of dried and sifted sand with 1 dram of shelled millet (3.32 ± 0.02 g standard error [SE], *n* = 10) mixed homogeneously throughout. This amount is within the range of commonly used amounts in foraging tray studies and unlikely to satiate an individual *P. leucopus* (e.g., Morris and Davidson 2000) and is therefore enough to capture changes in predation risk. A translucent white plastic lid was placed on each tray to prevent seed predation by birds or seed loss from adverse weather conditions; the lid was not expected to influence predation risk because it allowed light to pass through into the tray. One randomly chosen tray in each pair was then covered with an overturned 95-l black plastic container to provide artificial protection to rodents foraging in that tray. The container was propped 5–7 cm off the ground with logs under the long side of the container closest to the other tray in the pair to allow rodent access to the tray. Our use of experimental cover provides a standardized comparison between the 2 study habitats (Morris and Davidson 2000; Wolf and Batzli 2004) without the potential confounding that might be introduced by using naturally occurring shelters at each site.

Trays were placed at the sites, and millet was replaced daily for a 4-day acclimation period before data collection began. Trays were then checked daily over 2 4-day periods: 31 October–3 November and 7–10 November 2008. During each visit, seeds were sieved from the sand, and tray condition was noted. A tray was considered to have been foraged if it contained rodent feces, exhibited obvious signs of rodent digging (e.g., deep pits dug into the sand) or both. Trays were then restocked with fresh millet, which was thoroughly mixed with the sand. Collected seeds were dried at 50 °C for 12–16 h and weighed (mass is used to assess giving-up density because sand volume and starting seed mass are uniform; Brown 1988). On 3 November, trays were replenished with millet to provide a consistent foraging environment when data were not being collected.

Climate data, including average temperature, total precipitation, cloud cover, and weather conditions for each day, were collected from a weather station in St Charles, MO, approximately 25 km from the study area. The fraction of the moon illuminated each night was obtained from published tables available from the US Naval Observatory (<http://www.nws.noaa.gov/climate/index.php>).

Peromyscus leucopus abundance was measured at each site using live trapping. Four Sherman live traps were placed within 1 m of the original tray position. On 29 March 2009, the traps were baited with 5.5 g of raw rolled oats and propped open for a 1-day acclimation period. On 30 March 2009, all sites were visited to rebait and activate the traps. Traps were checked, emptied, rebaited, and reset at dawn each day from 31 March until 3 April 2009. Captured rodents were marked with a metal ear tag with a unique identification number and released near the site of capture; recaptured rodents were recorded and released.

Data analysis

Habitat characteristics were compared between sites that were invaded by *L. maackii* and uninvaded sites using 2-sample *t*-tests using the Satterthwaite approximation for unequal variances. Foraging tray data were examined using a repeated-measures mixed-model analysis of covariance (Littell et al. 1996) evaluating giving-up densities in both trays at each site. The model treated *L. maackii* treatment (i.e., invaded and uninvaded), cover, and week as fixed effects, and moonlight was evaluated as a covariate. Week was included in the model to account for temperature and weather changes across the study period. Each experimental site was modeled as a random effect, treating site as the subject in a repeated-measures design and using compound symmetry as the structure for modeling covariance among observations taken at a site on different days. We only use observations from pairs of trays where at least 1 of the trays exhibited signs of foraging for analysis (see Results), excluding 2 invaded and 3 uninvaded sites where there was no foraging activity at any point during the study. Analysis began using the most complex model (i.e., 4-way interaction of *L. maackii* treatment, cover, week, and moonlight), removing interaction terms from the model if they were not significant at $P > 0.15$. This procedure yielded the same results as building the model and excluding terms based on information-theoretic approaches such as Akaike's information criterion. Weather data were analyzed by *t*-tests comparing variables over time. Rodent abundance data were analyzed using *t*-tests to compare the total number of unique captures at invaded versus uninvaded sites. All analyses were conducted using SAS 9.1 (Littell et al. 1996); all means are presented ± 1 SE.

RESULTS

Habitat characteristics and weather data

Of the 4 habitat characteristics measured at each of 6 invaded and 6 uninvaded sites, only the average number of *L. maackii* individuals was significantly different, being 88 times greater in invaded sites (invaded site mean = 2.64 ± 0.39 SE, uninvaded site mean = 0.03 ± 0.03 SE, $P < 0.001$). Average light intensity at 1 m above ground, average light intensity at ground level, and average amount of leaf litter were not significantly different between the invaded and uninvaded sites ($P = 0.677, 0.238, \text{ and } 0.139$, respectively). We found significant differences between weeks in average temperature (week

1 = $13.57 \text{ }^\circ\text{C} \pm 0.057$ SE, week 2 = $4.13 \text{ }^\circ\text{C} \pm 1.56$ SE, $P < 0.001$) and mean cloudiness (measured as proportion of night described as overcast; week 1 = 0.00 ± 0.00 SE, week 2 = 0.32 ± 0.08 SE, $P = 0.003$).

Characterizing foraging activity

We collected 192 samples from 12 sites over 2 4-day sessions; 90 samples were taken from pairs of trays where at least one tray exhibited signs of foraging activity. Foraging was observed at 7 of the 12 study sites: 4 invaded sites and 3 uninvaded sites. On average, 80% of trays at each of the foraged sites were foraged during each of the 8 days of the study. Statistical results for habitat comparisons among invaded and uninvaded sites were qualitatively identical if only sites where foraging was observed were used. Although foraging was not observed at 2 invaded sites and 3 uninvaded sites, there was no significant difference in habitat variables between sites with and without foraging (*t*-test, all $P > 0.46$). Our method of classifying trays was highly effective for judging whether foraging occurred; foraged trays had significantly lower masses of millet left (1.91 ± 0.09 g SE) than both control samples (3.32 ± 0.02 g SE, $P < 0.001$) and nonforaged trays (3.15 ± 0.01 g SE, $P < 0.001$), and there were no significant differences between nonforaged and control millet samples ($P = 0.33$).

Foraging behavior and *L. maackii*

There was no significant main effect of *L. maackii* treatment, presence/absence of artificial cover, moonlight or week on *P. leucopus* giving-up densities (Table 1). However, the interactions of treatment and cover ($F_{1,35.7} = 5.48$, $P = 0.025$), moonlight and cover ($F_{1,58.9} = 5.44$, $P = 0.023$), and week and cover ($F_{1,61.9} = 6.10$, $P = 0.016$) were significant; the effect of cover was most pronounced during the first week (Figure 1). The interaction between moonlight and week was not significant ($F_{1,6.21} = 0.60$, $P = 0.469$).

The 3-way interaction between *L. maackii* treatment, cover, and moonlight was significant ($F_{2,57.3} = 3.26$, $P = 0.046$). The 3-way interaction of *L. maackii* treatment, cover, and week was not significant at $\alpha = 0.05$ ($F_{2,62.4} = 2.65$, $P = 0.078$), although the significant differences due to cover in the first week were largely due to foraging in uninvaded sites (Figure 1). We found no significant differences between covered and uncovered trays as moon illumination increased in the invaded (i.e., high-density *L. maackii*) plots, but there were differences in the uninvaded plots (Figure 2). In invaded plots, *P. leucopus* foraged to slightly lower giving-up densities

Table 1

Analysis of variance table for rodent giving-up densities in foraging trays at sites that experienced foraging activity only (4 high and 3 low *Lonicera maackii* sites), $n = 90$ observations

Effect	Num df	Den df	<i>F</i>	<i>P</i>
<i>L. maackii</i> treatment	1	12.1	0.13	0.723
Artificial cover	1	35.7	0.80	0.377
Week	1	2.5	0.04	0.864
Moonlight	1	8.8	0.67	0.436
<i>Lonicera</i> treatment \times cover	1	35.7	5.48	0.025
Cover \times week	1	61.9	6.10	0.016
Moonlight \times cover	1	58.9	5.44	0.023
Moonlight \times week	1	6.21	0.60	0.469
<i>Lonicera</i> treatment \times cover \times week	2	62.4	2.65	0.078
Moonlight \times <i>Lonicera</i> treatment \times cover	2	57.3	3.26	0.05

\times Indicates an interaction between 2 effects.

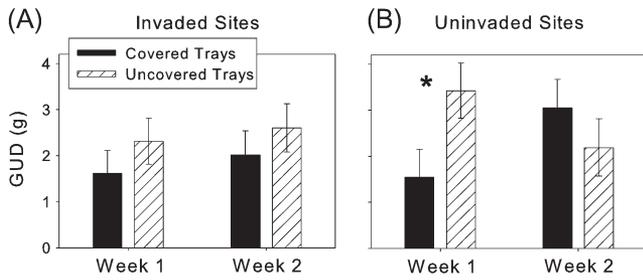


Figure 1 Effects of week and artificial cover on giving-up densities in foraging trays in sites invaded by *Lonicera maackii* and uninvaded sites. Week 2 had more cloud cover and lower temperatures (see Results). Results are based on mixed-model analysis of covariance (Table 1, $n = 90$ observations). Mean giving-up densities ± 1 SE are shown; an asterisk indicates significant differences between covered and uncovered trays ($P < 0.05$).

in the covered trays, but their preference for artificial cover did not change with increasing moon illumination. For uninvaded sites, in low (proportion of moon illuminated = 0.13, $F_{1,21.1} = 2.25$, $P = 0.148$) and medium (proportion of moon illuminated = 0.43, $F_{1,5.81} = 1.61$, $P = 0.253$) moon illumination, there was no significant difference between covered and uncovered tray giving-up densities (both $P > 0.15$; Figure 2). However, in high levels of moonlight (proportion of moon illuminated = 0.76), there was a strong preference for covered trays over uncovered trays (Figure 2; $F_{1,23.2} = 8.05$, $P = 0.009$) in uninvaded sites.

Rodent abundance

We caught 42 rodents over 196 trap nights; *P. leucopus* was the only species captured. Twenty-four mice were captured at invaded sites, and 18 were captured at uninvaded sites; no mice were captured at more than one site. There was no significant difference between the mean number of individual rodents captured among the 2 *L. maackii* treatments ($P = 0.47$). There was a strong trend of a greater average number of *P. leucopus* at sites where foraging was observed (0.219 ± 0.058 individuals) than at sites where no foraging was observed (0.06 ± 0.069 individuals; $P = 0.059$).

DISCUSSION

Our study provides evidence that invasive plants can have important effects on native animal behavior. Exotic *L. maackii*

interacted with other indirect indicators of risk to alter the antipredator behavior of native *P. leucopus*: the foraging activity of *P. leucopus* in areas dominated by *L. maackii* depended on moon illumination, a well-known indirect cue of predation risk, in addition to the presence of shrub cover. These findings have several important implications: 1) they demonstrate that invasive plants may alter the perceived, and potentially realized, predation risk for foraging animals; 2) they provide some of the first evidence that invasive plants may benefit from rodent-mediated apparent competition by forming refuges that seed predators may use while depleting other seeds of native species; and 3) they suggest that the effects of invaders on risk may be cryptic because they interact with other factors that influence risk.

Lonicera maackii affected rodent antipredator behavior by causing rodents to change foraging preferences based on the presence or absence of the invasive shrub. Rodents showed a stronger preference for trays under artificial cover that provided predator protection when they experienced habitat and abiotic conditions that provided stronger indirect cues for predation risk (Figure 2). Our observations illustrate that invasive plants can have complex indirect effects on native consumers, affecting consumer behavior and possibly having cascading effects through different trophic levels (Orrock et al. 2010). Plants have been demonstrated to affect rodent behavior in past studies because of varying foliage profile structure (M'Cluskey and Lajoie 1975) and diverse structural habitats (Mandelik et al. 2003), which alter perceived and actual risk of predation during foraging. This change in foraging behavior may then increase consumer pressure on native plants (Orrock et al. 2010). In the *L. maackii* system we studied, previous work has illustrated that *L. maackii* may increase rates of seed attack by granivores (Meiners 2007). Our work provides a mechanistic basis for this change in seed predation pressure by showing that rodent behavior is altered in invaded habitats. This suggests that rodents may facilitate *L. maackii* invasion by depleting stores of native seeds in *L. maackii* refuges and releasing invasive seeds from resource competition, an interaction known as apparent competition (Veech 2001; Meiners 2007; Orrock et al. 2008, 2010).

In addition to the presence of invasive shrub cover, several other variables and interactions were significant in affecting rodent foraging (Table 1), particularly week (Figure 1) and moon illumination (Figure 2). Further analyses suggest that temperature and cloudiness may have been important in determining the interaction between week, cover, and whether sites were invaded by *L. maackii*. Nighttime temperature, which has been shown to reduce rodent foraging activity (Orrock and Danielson 2009), was lower in week 2. In week 1, when temperatures were higher, there were significant differences in foraging in covered trays, but this was largely restricted to uninvaded sites (Figure 2). Moreover, temperature may also interact with cloud cover (Orrock and Danielson 2009), producing potentially complex variation in rodent foraging that would be profitable avenues of future research.

Our results illustrate that a commonly observed component of rodent foraging, that is, more risk-averse foraging during periods of increased moon illumination (e.g., Kotler et al. 1991; Longland 1994; Mandelik et al. 2003; Orrock et al. 2004), is also affected by the presence of an invasive plant species (Figure 2). This result further highlights that invasive plants may interact with commonly observed (and temporally variable) behaviors, suggesting that the reduction in risk provided by *L. maackii* is contingent on several other characteristics of the foraging environment (e.g., temperature and moon illumination) and the state of the forager. For example, rodents have been observed to have less consideration for predation risk when food resources are scarce (McCormick

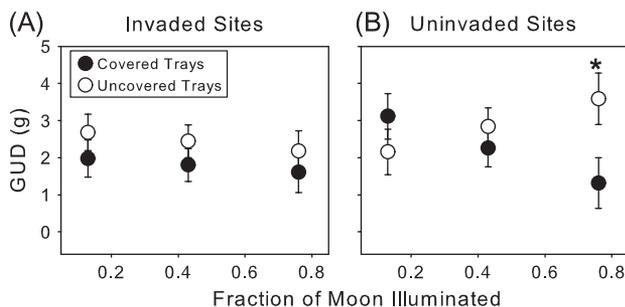


Figure 2 Effects of moon illumination and artificial cover on giving-up densities in foraging trays in sites invaded by *Lonicera maackii* and uninvaded sites. Results are based on mixed-model analysis of covariance (Table 1, $n = 90$ observations) showing the average giving-up densities within the treatments that occur at 3 representative levels of moon illumination. Mean giving-up densities ± 1 SE are shown; an asterisk indicates significant differences between covered and uncovered trays ($P < 0.05$).

and Meiners 2000). Because our study was conducted in the late autumn when natural food sources may have been less abundant, mice may have been more willing to forage in riskier areas in order to acquire food (White and Geluso 2007). As such, although we observed significant interactive effects of *L. maackii* cover on rodent foraging, *L. maackii* cover may have an even greater impact on rodent foraging at times of year when other foraging constraints are reduced, for example, when food resources are more plentiful. Moreover, changes in rodent foraging caused by *L. maackii* may interact with other effects of *L. maackii* on native food webs. For example, shading by *L. maackii* may reduce seed pollination and seed production of native plants (McKinney and Goodell, 2010). When coupled with increased seed predation due to changes in rodent behavior, low seed production would be expected to further increase the likelihood that *L. maackii* will have detrimental effects on native plants.

Because rodent foraging over the duration of our study limited the number of sites used in our analysis (i.e., 4 invaded and 3 uninvaded sites), it will be important to conduct additional studies to understand the generality of our results across broader spatial scales and document whether shifts in foraging behavior are widespread throughout the invaded range of *L. maackii*, which extends through much of the Eastern and Midwestern United States. Importantly, the number of sites in our study was sufficient to detect significant differences in rodent foraging due to *L. maackii*, as well as interactions between *L. maackii* and indirect indicators of predation risk (Table 1). Moreover, results of another rodent activity study conducted at 12 locations in the same study system provide strong support that the trends we observed are consistent across additional study areas: Using track plates to assay rodent activity density, experimental removal of *L. maackii* cover leads to increased rodent activity but only on nights when moon illumination is high (Dutra H, personal communication).

In demonstrating that an invasive plant can alter the behavior of native rodents, our study illuminates several additional areas for future research. Behavioral changes caused by *L. maackii* may also affect other ecological interactions, such as nest predation (e.g., Schmidt and Whelan 1999; Rodewald et al. 2010), pollination (McKinney and Goodell, 2010) and disease risk (Allen B, personal communication), with largely unknown consequences. Future work is also needed to understand whether changes in antipredator behavior yield differential attack rates on native plants, that is, whether the shift in behavior yields apparent competition (Meiners 2007; Orrock et al. 2008) and how temporal variation in environmental conditions and forager state are likely to influence the degree to which invasive species alter the behavior of native animals (McCormick and Meiners 2000). Our work suggests that an invasive plant may alter the behavior of a native rodent consumer; if behavioral shifts are a common result of plant invasions (Orrock et al. 2010), invasive plants may have a variety of important, yet cryptic, effects on individuals, populations, and communities.

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