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Original Article

Invasive shrubs modify rodent activity timing, revealing a consistent behavioral rule governing diel activity

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Animals adjust the timing of their activity to maximize benefits, such as access to resources, and minimize costs, such as exposure to predators. Despite many examples of invasive plants changing animal behavior, the potential for invasive plants to alter the timing of animal activity remains unexplored. In eastern North America, invasive shrubs might have particularly strong effects on animal activity timing during spring and fall, when many invasive shrubs retain their leaves long after native species' leaves senesce. We experimentally removed an invasive shrub (buckthorn, *Rhamnus cathartica*) and monitored the activity timing of a ubiquitous small-mammal species (white-footed mouse, *Peromyscus leucopus*) in spring, summer, and fall. We captured nearly 3 times as many *P. leucopus* in plots invaded by *R. cathartica* compared with plots with *R. cathartica* removed, and *P. leucopus* were captured 2 h earlier in invaded plots. Regardless of invasion treatment, *P. leucopus* appear to follow a common rule to set activity timing: *P. leucopus* were only active below a threshold of ground-level moonlight illuminance (0.038 lux). Diel and monthly lunar cycles play an important role in regulating small-mammal activity, but our data suggest that decreased light penetration dampens the influence of moonlight illuminance in habitats invaded by *R. cathartica,* allowing *P. leucopus* to remain active throughout the night. By changing the temporal niche of ubiquitous native animals, invasive shrubs may have unappreciated effects on many ecological interactions, including processes that alter community diversity and affect human health.

Key words: **extended leaf phenology, habitat structure, lunar cycle, moonlight illuminance, *Peromyscus leucopus*, *Rhamnus cathartica*.**

INTRODUCTION

Timing is fundamental to organismal fitness: procuring resources and finding mates, while avoiding competitors, parasites, and predators requires being in the right place at the right time (Kronfeld-Schor and Dayan 2003). Activity timing (i.e., temporal activity patterns) also has important ecological implications and can influence the distribution and abundance of populations (Williams et al. 2017), the outcome of competition among species (Abu Baker and Brown 2014), the strength of plant-herbivore interactions (Yang and Rudolf 2010), prey avoidance of predators (Fox and Bellwood 2011; Monterroso et al. 2013), and host–pathogen dynamics (Altizer et al. 2011). Given the importance of activity timing for ecology and evolution (Kronfeld-Schor and Dayan 2003), and evidence that habitat degradation can lead to large-scale changes in activity timing and subsequent ecological interactions (Bennie et al. 2014; Gaston et al. 2015; Gaynor et al. 2018; Hopkins et al. 2018), identifying environmental factors that may rapidly change the timing of activity is a pressing challenge.

Invasive plants are widespread in diverse habitats throughout the world (Vilà et al. 2011), where they often alter the physical structure and community composition of habitats in their introduced range (Pearson 2009). Changes in habitat structure caused by invasive plants are known to elicit behavioral changes in native animals by either increasing (Smith-Ramesh 2017) or decreasing predation risk (Orrock et al. 2010). These shifts in habitat structure may be highly seasonal. For example, throughout eastern North America, extended leaf phenology of invasive shrubs produce stark changes in habitat structure by providing a dense canopy during spring and fall that often does not exist in uninvaded habitats (Fridley 2012; Smith 2013), suggesting that invasive shrubs might have disproportionately strong effects on animal behavior during these seasons (Bartowitz and Orrock 2016). However, evidence that extended leaf phenology of invasive plants causes behavioral shifts in native animals remains rare (Smith 2013), despite an understanding that

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the dense growth of invasive plants can disrupt important cues in summer (Mattos and Orrock 2010; Conley et al. 2011). For example, small mammals often perceive moonlight as an indirect cue of predation risk (Orrock et al. 2004). Small mammals may consequently restrict activity at times with bright moonlight, such as nights with a full moon (Kotler et al. 2010), cloudless nights (Connolly and Orrock 2017), or the hours between moonrise and moonset (Upham and Hafner 2013). However, the thick cover provided by invasive shrubs can weaken small mammal responses to moonlight (Mattos and Orrock 2010), suggesting that the novel predation refuge created by the mismatch between native tree and invasive shrub leaf phenology could alter the timing of activity in native animals. Such unappreciated shifts in activity timing could alter interactions among small mammals and other species (e.g., ectoparasites that carry zoonotic disease) and may help explain how invasive plants modify human disease risk (Allan et al. 2010).

We coupled an experimental removal of an invasive shrub (buckthorn, *Rhamnus cathartica*) with 2 complimentary methods of tracking activity timing to evaluate whether invasive shrubs can cause shifts in activity timing of a nocturnal small mammal species (white-footed mouse, *Peromyscus leucopus*). We hypothesized that 1) the amount of moonlight reaching the forest floor would influence that timing of *P. leucopus* activity; 2) *P. leucopus* would become active earlier in habitats invaded by *R. cathartica*; and 3) the effect of *R. cathartica* on *P. leucopus* activity timing would be strongest in spring and fall when protective cover is greater in invaded plots. Our results provide an important new insight into the effects of invasive plants: seasonal changes in habitat structure created by invasive plants cause a profound shift in the timing of activity for native small mammals. Moreover, these data reveal a simple, but unappreciated behavioral rule that underpins the observed shift in activity timing, which may provide insight into small-mammal behavior across a broad range of habitats.

METHODS

This study was conducted at the University of Wisconsin Arboretum in Madison, WI in a closed-canopy deciduous oak-hickory forest. *Rhamnus cathartica* is widespread throughout the forest understory. In summer 2014, sixteen 20- × 20-m plots were delineated, and 8 were randomly chosen to have all invasive shrubs removed (Guiden and Orrock 2017). *Rhamnus cathartica* removal decreased stem density, but the treatments do not differ in canopy composition, woody debris availability, or leaf litter depth (Supplementary Material S1). Since 2014, plots with *R. cathartica* removed have been monitored annually to remove any encroaching *R. cathartica* seedlings.

We measured light penetration 0.5 m above ground level at 3 locations near the plot center to capture variation in the predation risk perceived by small mammals (Mattos and Orrock 2010). Light penetration was measured as the amount of photosynthetically active radiation (PAR) reaching the forest floor divided by PAR reaching a nearby open area with no canopy. Because we expected the protective cover provided by *R. cathartica* to exhibit strong seasonal dynamics (Smith 2013; Bartowitz and Orrock 2016), we repeated PAR measurements at the same locations in each plot 8 times, starting 7 April 2017 and ending 6 November 2017. PAR readings were taken in the same locations, at approximately the same time (within 1 h of solar noon) regardless of date. Standardizing the time and location of data collection and accounting for variation in ambient PAR allowed us to compare patterns of light penetration throughout the year. Light penetration was modeled as a quadratic function of *R. cathartica* invasion and day of year, with a random intercept for plot. To account for temporal autocorrelation among light penetration measurements, the model used a first-order autoregressive correlation structure (Pinheiro et al. 2017).

We assessed the magnitude and timing of small-mammal activity in each plot with one motion-activated infrared camera (Bushnell Essential E3, Overland Park KS, Supplementary Material S2) attached to a tree approximately 0.5 m above ground (Abu Baker and Brown 2014; Rowcliffe et al. 2014). Cameras were deployed for a total of six 5-day sessions, including 2 weeks in the spring (16 April–21 April, 1 May–6 May 2017), 1 week in the summer (25 June–30 June 2017), and 3 weeks in the fall (9 October–14 October, 28 October–1 November, 2 November–7 November 2017). Small mammals were baited to the cameras using raw, unsalted, husked sunflower seeds mixed with sand in a 23- × 23-cm aluminum pan placed approximately 5 m away from the camera. Seeds were replenished every 2 days if there was evidence of seed consumption at a foraging tray.

We used temporal activity distributions generated from camera data collected in the spring, summer, and fall to test the hypothesis that indirect effects of invasive *R. cathartica* are stronger in spring and fall than in summer. We developed separate kernel density functions of *P. leucopus* photograph time stamps in plots invaded by *R. cathartica* and plots with *R. cathartica* removed, for each of the 3 seasons when cameras were deployed (spring, summer, fall; $n = 6$ distributions). We compared *P. leucopus* activity distributions between *R. cathartica* treatments within each season by estimating the coefficient of overlap between temporal activity distributions in plots invaded by *R. cathartica* and plots with *R. cathartica* removed (Meredith and Ridout 2017). Coefficient of overlap values are bound between 0 and 1, with a value of 1 indicating perfect overlap between distributions. To test for significant differences in overlap between seasons, we generated bootstrapped confidence intervals around these estimates using 1000 bootstrap samples (Meredith and Ridout 2017).

We also monitored small-mammal activity using live-traps. At each plot, 4 live-traps (H.B. Sherman Traps, Inc., Tallahassee, FL) were baited with oats and set throughout the plot. Traps were baited and locked open for 1 night at the beginning of each live-trapping session, allowing animals to acclimate to traps. Following this prebaiting period, traps were deployed for 4 nights, for a maximum of 16 trap-nights per plot per session. We conducted one 4-night live-trapping session in the spring (3 May–6 May 2017) and 2 sessions in the fall (11 October–14 October, 29 October–1 November 2017). In all sessions, traps were prebaited (deployed with bait, but locked open to allow small mammals to acclimate to traps) for 1 night before recording data. We constructed a linear-mixed effects model (Bates et al. 2015) to describe the number of *P. leucopus* live-captures per 16 trap nights at each plot which provides an index of small-mammal activity (Orrock and Danielson 2005), as a function of *R. cathartica* removal (*R. cathartica* invaded, *R. cathartica* removed), season (spring, fall), and a *R. cathartica* × season interaction with a random intercept for plot.

We estimated the time at which captured animals entered traps based on changes in temperature driven by small-mammal body heat (Supplementary Material S3) using an approach that has been validated for several small-mammal species, including *Peromyscus* spp. (Orrock and Connolly 2016). Because body mass can affect activity timing (Connolly and Orrock 2017) and *P. leucopus* body mass spanned a much greater range in plots invaded by *R. cathartica* compared with plots with *R. cathartica* removed (see Results, Supplementary Material S4), we only evaluated individuals of similar body mass in both removal treatments (body mass range: 17.5–25 g, Supplementary Material S4). Activity timing might also differ as a function of individual capture history (Joly and Zimmermann 2011). To account for individual capture history, we only examined trap-entry times from the first capture of each individual *P. leucopus*.

To test our hypothesis that small-mammal activity is driven by variation in indirect cues of predation risk (Mattos and Orrock 2010; Connolly and Orrock 2017), we assessed whether temporal variation in *P. leucopus* activity was associated with temporal variation in moonlight reaching the forest floor. Importantly, moonlight exhibits both monthly (i.e., lunar phases) and diel (i.e., time of moonset and moonrise) cycles. We therefore estimated the instantaneous moonlight illuminance at the time of each capture event in order to account for both changes in moon phase and the timing of moon rise (Austin et al. 1976; Upham and Hafner 2013). To estimate moonlight illuminance perceived by small mammals at the forest floor, we multiplied moonlight illuminance by light penetration (relative PAR). We modeled moonlight illuminance reaching the forest floor at the time of capture as a function of *R. cathartica* removal, season, and a *R. cathartica* removal × season interaction using Cox's proportional hazard model with a random intercept term for plot (Therneau 2015). We then determined whether *R. cathartica* altered *P. leucopus* activity patterns by modeling estimated trap-entry time (hours after sunset) as a function of *R. cathartica* removal, season, and a *R. cathartica* removal × season interaction using a Cox's proportional hazard model with a random intercept term for plot.

RESULTS

In all plots, light penetration was lowest during summer (day of year^2: $F_{1,364} = 88.82$, $P < 0.0001$). Forest floor light penetration was on average 47.8% lower in plots invaded by *R. cathartica* (0.162 ± 0.024) relative to plots with *R. cathartica* removed (0.338 ± 0.024, $F_{1,14} = 22.29$, $P = 0.003$), but this effect was strongest in the spring and fall (*R. cathartica* × day of year^2: $F_{1,364} = 7.41$, $P = 0.007$, Figure 1a). Seasonal patterns in light penetration were strongly linked with changes in the timing of *P. leucopus* activity. We collected 1315 photographs of *P. leucopus* across 576 camera trap-nights. *Rhamnus cathartica* removal decreased the number of *P. leucopus* photographs, and photographs were recorded later in the night in plots with *R. cathartica* removed (Supplementary Material S2). Kernel distributions of *P. leucopus* photograph times overlapped much more in summer (coefficient of overlap 95% confidence interval: 0.559–0.866) than in spring (0.148–0.228) or fall (0.076–0.546, Figure 1b).

We captured 23 individual *P. leucopus* in live-traps, as well as a single *Tamias striatus* (eastern chipmunk) that was excluded from further analysis. *Peromyscus leucopus* captures were nearly 3 times greater in plots invaded by *R. cathartica* (14.31 ± 2.08 captures per 100 trap nights) than plots with *R. cathartica* removed (5.31 ± 2.08 captures per 100 trap nights, $F_{1,14} = 8.56$, $P = 0.01$). *Peromyscus leucopus* activity was also strongly seasonal, as the number of total captures of *P. leucopus* was nearly 3 times greater in spring (14.64 ± 2.13 captures per 100 trap nights) than fall (4.98 ± 1.62 captures per 100 trap nights, $F_{1,30} = 16.31$, $P = 0.0003$); there was no significant *R. cathartica* × season interaction ($F_{1,30} = 0.81$, $P = 0.37$).

Although ground-level moonlight illuminance exhibited considerable temporal variation within and among trap-nights, *P. leucopus* were captured most frequently at times when little light reached the forest floor, regardless of *R. cathartica* removal ($\chi^2 = 0.62$, d.f. = 1, $P = 0.43$, Figure 1c). *Peromyscus leucopus* were captured during brighter periods in the spring (0.021 ± 0.002 lux) compared with the fall (0.005 ± 0.004 lux, season: $\chi^2 = 13.88$, d.f. = 1, $P = 0.002$) due to increased canopy openness during spring, but there was no *R. cathartica* × season interaction ($\chi^2 = 0.18$, d.f. = 1, $P = 0.67$). Importantly, *P. leucopus* were never captured when ground-level moonlight illuminance was greater than 0.037 lux, despite ground-level moonlight illuminance reaching 0.085 lux in plots with *R. cathartica* removed (Supplementary Material S3).

Peromyscus leucopus entered traps more than 2 h earlier in plots invaded by *R. cathartica* (mean trap-entry time: 3.09 ± 0.46 h after sunset) compared with plots with *R. cathartica* removed (5.47 ± 0.98 h after sunset; $\chi^2 = 4.86$, d.f. = 1, $P = 0.03$, Figure 1d). Although there was no significant *R. cathartica* removal × season interaction ($\chi^2 = 0.46$, $P = 0.50$), *P. leucopus* entered traps more than 1 h earlier in spring (3.60 ± 0.48 h after sunset) compared with fall (4.96 ± 0.97 h after sunset; $\chi^2 = 3.79$, $P = 0.05$). Because trap success was low in removal plots, we repeated this analysis using only invaded plots. Using only invaded plots, this difference in timing was still evident: *P. leucopus* trap-entry times were still significantly earlier in spring compared with fall (pairwise comparison: $z = 2.04$, $P = 0.04$).

DISCUSSION

Our results demonstrate that a widespread invasive shrub generates significant shifts in the activity timing of a ubiquitous native animal. *Peromyscus leucopus* in our study area appear to use a common behavioral rule to initiate activity (become active when moonlight illuminance drops below a threshold value), entering traps at times characterized by low predation risk regardless of the presence of invasive shrubs (Figure 1c). This same behavioral rule leads to very different activity patterns in habitats with and without invasive shrubs. Because invasive shrubs caused stark differences in habitat structure (Figure 1a), *P. leucopus* were photographed at foraging trays earlier during spring and fall (Figure 1b). *Peromyscus leucopus* also entered traps more frequently and entered traps earlier in plots invaded by *R. cathartica* compared to plots with *R. cathartica* removed during spring and fall (Figure 1d).

These results have 3 important implications for the ecology and management of invasive species. First, by altering the timing of animal activity, invasive shrubs may alter the strength of species interactions by increasing overlap between *P. leucopus* and its competitors or pathogens (Kronfeld-Schor and Dayan 2003). Second, the strong effect of body mass and light penetration on *P. leucopus* activity timing demonstrate that intrinsic and extrinsic factors can produce dynamic diel activity patterns, suggesting that quantifying activity patterns may require multiple measurements that capture this variation. Third, seasonal shifts in activity timing driven by invasive shrubs may lead to overlooked changes in important ecological interactions, especially in temperate regions where invasive shrubs exhibit extended leaf phenology (Fridley 2012). Because temporal niches are fundamentally important to ecology and evolution, and because invasive plants are changing plant and animal communities worldwide (Vilà et al. 2011), understanding shifts in the timing of animal activity in invaded habitats could provide a powerful means of predicting and mitigating the negative effects of invasive plants.

Invasive shrubs alter the timing of animal activity

Mammals can adjust the timing of their activity in highly modified habitats, such as habitats with artificial lighting (Bennie et al.

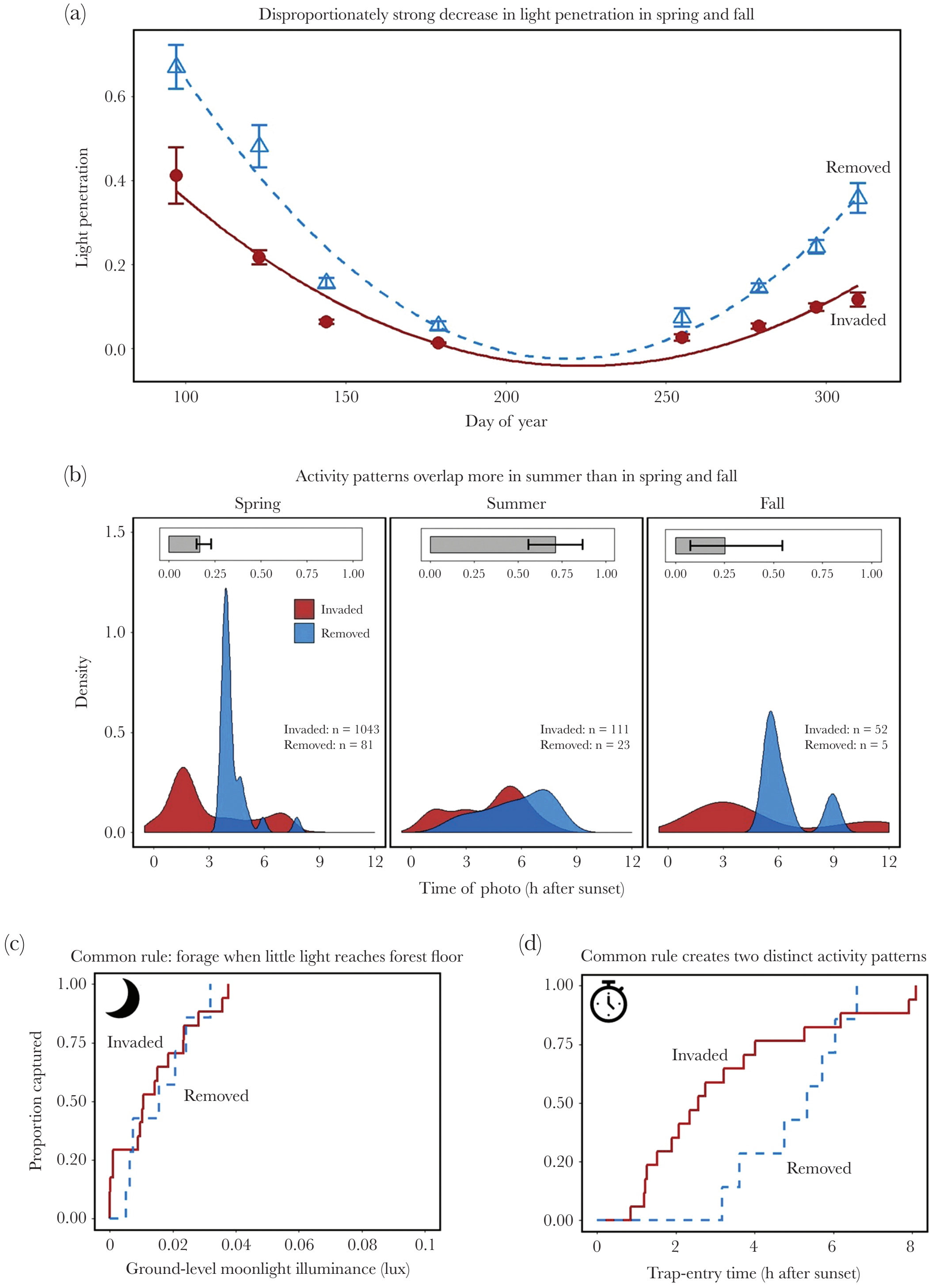

Figure 1

Rhamnus cathartica alters the timing of *Peromyscus leucopus* during spring and fall. (a) Forest floor light penetration, a measure of protective cover, measured 0.5 m above ground. Points represent least-squared means ± s.e. of relative PAR measurements recorded in 8 plots invaded by *R. cathartica* (red circles) and 8 plots with *R. cathartica* removed (blue triangles) on 8 dates between 7 April and 6 November 2017. Curves represent predictions from a quadratic model describing light penetration as a function of date and *R. cathartica* removal. (b) Temporal distribution of *P. leucopus* activity recorded by motion-activated cameras in spring, summer, and fall. Distributions were constructed by pooling *P. leucopus* observations from 8 plots invaded by *R. cathartica* and 8 plots with *R. cathartica* removed. Bars within each panel represent coefficient of overlap in distributions between treatments, and error bars represent bootstrapped 95% confidence intervals. Sample sizes refer to the number of photographs used to build each distribution. (c) Ground-level moonlight illuminance (moonlight illuminance × light penetration), an instantaneous measure of perceived risk at the time of *P. leucopus* capture (n = 23). Moonlight illuminance accounts for both changes in moon phase and changes in the timing of moonrise/moonset. Perceived risk was not significantly different between invaded habitats and habitats with *R. cathartica* removed ($P = 0.43$). *Peromyscus leucopus* were often captured during times of little to no risk (maximum ground-level moonlight illuminance: 0.085). (d) *Peromyscus leucopus* trap-entry time (hours after sunset) as a function of *R. cathartica* removal ($P = 0.04$).

2014; Hopkins et al. 2018) and frequent human activity (Gaynor et al. 2018). Our results show an additional, previously unappreciated pathway by which both anthropogenic and natural changes in habitat can alter the timing of activity: nocturnal small mammals become active earlier and remain active longer in the presence of invasive plants (Figure 1b), likely because less moonlight reaches the forest floor (Figure 1c). Although all plots experienced the same moonlight illuminance at a given moment, seasonal differences in light penetration between invaded and uninvaded treatments (Figure 1a) produced distinct activity patterns in habitats with and without invasive shrubs (Figure 1b, d). Seminal studies as well as synthetic reviews have found variable effects of moonlight on animal activity in diverse habitats across the world (Orrock et al. 2004; Upham and Hafner 2013; Prugh and Golden 2014), and our data provide an important new perspective for this research. These data demonstrate the need to account for 1) interactions between moon phase and seasonal changes of habitat structure and 2) night-to-night variation in the timing of moonrise and moonset in order to accurately assess how prey perceive moonlight as an indirect cue of predation risk. Explicitly considering the effects of habitat structure and nightly changes in the timing of moonrise or moonset may increase ecologists' ability to explain temporal variation in a wide range of ecological processes, such as predation (Clarke 1983) or competition (Abu Baker and Brown 2014).

Changes in *P. leucopus* activity timing may also affect the strength of interspecific interactions in invaded habitats (Kronfeld-Schor and Dayan 2003; Abu Baker and Brown 2014). For example, small mammals foraging earlier in invaded habitats (Figure 1d) may be more likely to encounter questing ticks (Duffy and Campbell 1994), providing one potential explanation for why invasive shrubs are associated with elevated risk of tick-borne illnesses in humans (Allan et al. 2010). Our results also suggest that by becoming active earlier, invasive shrubs might alter competitive interactions among small mammals. Temporal niche partitioning promotes coexistence of otherwise similar small-mammal species (Abu Baker and Brown 2014), but longer *P. leucopus* activity windows in invaded habitats (Supplementary Material S2) could eliminate an important temporal refuge for other small-mammal species. This could impose fitness costs on nocturnal competitors of *P. leucopus*, such as *P. maniculatus* or *Myodes gapperi* (Bruseo and Barry 1995; Lemaître et al. 2010), and, in extreme cases, competitive exclusion (Bennie et al. 2014). Our results suggest that plant-mediated shifts in activity timing might increase temporal overlap among competitors and may be one unappreciated mechanism contributing to the large number of animal extinctions caused by invasive plants (Clavero and García-Berthou 2005).

Activity patterns are influenced by both intrinsic and extrinsic factors

The effects of invasive shrubs on the timing of activity may vary among individual *P. leucopus*. A number of factors, such as body mass, social rank, and nutrition, can affect the risk animals are willing to accept in order to forage (McNamara and Houston 1992; Clark 1994). Our finding that larger individuals were associated with later trap-entry times (Connolly and Orrock 2017; Supplementary Material S4) could represent high-fitness individuals "playing it safe," delaying foraging to pursue other opportunities, such as reproduction or territory defense (McNamara and Houston 1992). However, given our low sample size of *P. leucopus* in plots with *R. cathartica* removed, it remains unclear if *R. cathartica* removal changes the shape of state-dependent foraging decisions in *P. leucopus* (i.e., changes in the payoff matrix, Trimmer et al. 2017). By increasing overall predation risk, *R. cathartica* removal may lead to smaller responses of mass or fitness versus foraging time.

Although our results demonstrate a strong effect of invasive shrubs on the timing of small-mammal activity, it is unknown whether this effect could vary across spatial gradients of invasion history. Because *P. leucopus* activity timing is sensitive to changes in habitat structure (i.e., light penetration, Figure 1a), small mammals may not shift the timing of their activity until a thick canopy develops, often several years after invasive plants disperse to a new habitat (Shields et al. 2014a). Moreover, because light penetration appears to drive shifts in the timing of *P. leucopus* activity, it is possible that dense growth of native plants (e.g., *Rubus* spp. in forest canopy gaps) may also elicit similar responses in animal activity timing. Comparing shifts in the timing of small mammal activity timing along invasion fronts to habitats with a long history of invasion could therefore provide an important tool to inform conservation efforts regarding when and where invasive shrubs will likely have the largest effects on animal behavior (Schlaepfer et al. 2002).

Indirect effects of invasive shrubs are most pronounced in spring and fall

Invasive plants can have strong effects on animal behavior (Mattos and Orrock 2010) (Figure 1d), but important behavioral changes in native animals during spring and fall due to extended leaf phenology of invasive plants are often overlooked (Smith 2013; Bartowitz and Orrock 2016). Our finding that invasive plants have strong, seasonal effects on animal activity may help resolve the discrepancy between studies that have found strong effects of invasive plants on animal behavior and those that have not. For example, studies in temperate forests that have found no effect of invasive plants on rodent activity (Shields et al. 2014b; Bartowitz and Orrock 2016) are often conducted only in the summer, when our results demonstrate that the effects of invasive shrubs on protective cover are weakest (Figure 1a). Small mammal activity timing was also significantly earlier in invaded habitats during the spring, but our *R. cathartica* removal treatment had little effect on activity timing during the summer (Figure 1b). Although diel patterns of activity during fall and spring were statistically similar (Figure 1b), the low number of *P. leucopus* photographs and live-captures during fall limits our inference regarding the effects of invasive plants in this season. Collecting more robust activity timing data during fall remains an important step in understanding seasonal variation in the effect of *R. cathartica* on diel activity patterns.

Developing a better understanding of the indirect effects of invasive shrubs on consumer behavior in spring and fall is critical, as these seasons encompass important life history events for both small mammals and the species with which they interact. For example, mating systems can be strongly influenced by diel fluctuations in environmental conditions (Ellison et al. 2012). Because the thick canopy of *R. cathartica* dampens diel fluctuations in moonlight, the resulting longer windows of activity (Figure 1b) could possibly increase *P. leucopus* promiscuity during spring (Godwin 1995; Bryja and Stopka 2005; Pita et al. 2011), which could increase effective population sizes (Caro 2007). Additionally, invasive shrubs may disrupt mutualisms between masting trees and rodents during fall. Gray squirrels (*Sciurus carolinensis*) disperse seeds to open high-risk microhabitats (Steele et al. 2014), but the abundance of cover provided by invasive species (Figure 1a), coupled with increased small-mammal activity in invaded habitats during autumn and spring (Figure 1b, Supplementary Material S3), could decrease the likelihood that dispersed seeds can persist until germinating (Bartowitz and Orrock 2016; Guiden and Orrock 2017). This elevated pressure from seed predators during fall and spring could select for seed traits such as early germination (Steele et al. 2006). Effective management of native plants may therefore require a clear understanding of how invasive shrubs alter animal behavior during in spring and fall.

CONCLUSIONS

Predation risk can be an important driver of diel activity patterns (Courbin et al. 2019; Gaynor et al. in press), but human activity may reduce predation risk, causing shifts activity patterns that alter subsequent species interactions (Guiden et al. forthcoming). Although many natural areas are becoming artificially bright at night (Bennie et al. 2014; Gaston et al. 2015), our data demonstrate that invasive shrubs can have the opposite effect: previously important sources of natural light, such as moonlight, no longer influence the behavior of native animals due to the thick canopy of invasive shrubs. We show that small mammals in invaded habitats experience artificially dark conditions, causing different diel activity patterns compared with habitats with invasive shrubs removed. This change in the timing of activity provides another example of invasive shrubs disrupting behaviors of native animals (Conley et al. 2011; Guiden and Orrock 2017). Identifying why invasive shrubs alter the timing of small-mammal activity remains an important step for future research. In addition to predation risk, seasonal pulses of resources may alter the timing of animal activity (Brown et al. 2001). Experimental manipulations of both food and habitat structure may therefore be necessary to parse out the effects of food subsidies and predation risk on activity timing (Orrock et al. 2015). Furthermore, the potential for experience to modify behavioral rules governing small-mammal activity timing remains unexplored (Schlaepfer et al. 2005), suggesting that future studies could examine how moonlight affects activity timing in animals that have been previously captured. Given the potential importance of diel activity patterns for ecological function and human health, ecologists must continue to investigate how invasive plants may alter the temporal niche of small mammals.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Authors contributions: P.W.G. and J.L.O. designed the study, collected and analyzed data, and wrote the manuscript.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Guiden and Orrock (2019).

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