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Rodents balancing a variety of risks: invasive fire ants and indirect and direct indicators of predation risk

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Abstract We used foraging trays to compare how oldfield mice, *Peromyscus polionotus*, altered foraging in response to the presence of fire ants, *Solenopsis invicta*, and in the presence of direct (predator urine) and indirect (sheltered or exposed microhabitat, moonlight, and precipitation) indicators of predation risk. Foraging reductions elicited by *S. invicta* were greater than reductions in response to well-documented indicators of risk (i.e., moonlit nights) and the presence of predator urine. The presence of *S. invicta* always led to reduced foraging, but the overall impact of *S. invicta* was dependent upon microhabitat and precipitation. When *S. invicta* was not present, foraging was greater in sheltered microhabitats compared to exposed microhabitats. *S. invicta* made sheltered microhabitats equivalent to more risky exposed microhabitats, and this effect was especially pronounced on nights without precipitation. The effect of *S. invicta* suggests that interactions with *S. invicta* may entail a potentially heavy cost or that presence of *S. invicta* may represent a more reliable indicator of imminent competition or predation compared to indirect cues of risk and predator urine. The presence of *S. invicta* led to reduced foraging under situations when foraging activity would otherwise be greatest (i.e., under vegetative cover), potentially reducing habitat quality for *P. polionotus* and the distribution of seeds consumed by rodents.

Keywords Behavior · Giving-up density · *Peromyscus polionotus* · Predation risk · *Solenopsis invicta*

Introduction

Understanding how prey recognize and respond to risk may provide insight into how predation risk affects prey fitness (Lima 1998), population dynamics (Lima 1998), and the structure of ecological communities (Schmitz et al. 1997). Rodents forage under risk of death from a variety of avian, reptilian, and mammalian predators. A large body of literature suggests that rodents are aware of risks during foraging, and modify their behavior accordingly. For example, rodents preferentially forage in sheltered microhabitats (often under vegetative cover), where the risk of avian predation is lower (e.g., Kotler et al. 1991). Rodents may avoid forest edges, where predation by vertebrates is greater (Morris and Davidson 2000) or forage more intensively close to escape routes (Thorson et al. 1998). Foraging may also be greater when precipitation or lack of moonlight reduces the ability of vertebrate predators to detect and capture rodents (Wolfe and Summerlin 1989; Kotler et al. 1991; Orrock et al. 2004).

Foraging by rodents may also be affected by the introduced fire ant, *Solenopsis invicta*, an invasive species found to affect a variety of invertebrates and vertebrates, including rodents (Masser and Grant 1986; Vinson 1997; Holway et al. 2002). In laboratory studies, deer mice, *Peromyscus maniculatus*, reduced time spent in foraging patches when *S. invicta* was present (Holtcamp et al. 1997). Similarly, Pygmy mice, *Baiomys taylori*, avoided the arm of a Y-maze with crushed *S. invicta* in behavioral trials (Lechner and Ribble 1996). In field studies, total captures of small mammals are often negatively related to the density of *S. invicta* mounds, although the relationship may vary depending upon the species of rodent and the spatial resolution of analysis (Killion and Grant 1993; Ferris et al. 1998). When abundance of *S. invicta* was experimentally reduced, new captures of *B. taylori* increased (Killion et al. 1995).

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Rodents may avoid *S. invicta* because interactions with it entail a cost: painful stings are the most likely outcome of a short-term interaction, making *S. invicta* a potentially potent competitor (via interference and exploitation) because fire ants also consume seeds consumed by rodents (Ready and Vinson 1995; Cothran et al. 1991). Previous studies have documented that rodents balance the costs of competition and predation, and that the strength of competitive interactions among rodents can be influenced by predation risk (Abramsky et al. 1998). Competition with *S. invicta* may be particularly risky because rodents that are not deterred by stings are more likely to be killed if *S. invicta* workers recruit nestmates. Given this evidence that *S. invicta* affects rodent activity (e.g., Lechner and Ribble 1996; Holtcamp et al. 1997), a profitable next step would be to determine how *S. invicta* is incorporated into other costs (e.g., exposure to predators) that rodents encounter during foraging. For example, if *S. invicta* is present in a foraging area, do rodents shift their behavior in ways that increase their susceptibility to vertebrate predators (Kotler et al. 1992)?

We examined how oldfield mice, *Peromyscus polionotus*, balance risks of predation with the risk of competitive, and potentially lethal, interactions with the invasive fire ant, *S. invicta*. High densities of *S. invicta* may increase the likelihood of interactions among *P. polionotus* and *S. invicta* in the field: approximately 7–100 *S. invicta* mounds can occur within the area of a single *P. polionotus* home range (Vinson 1997), with up to 300,000 *S. invicta* per mound (monogyne colonies; Vinson 1997). Previous work suggests that foraging by *P. polionotus* is affected by indirect measures of predation risk: mice forage more beneath vegetative cover compared to exposed areas outside of cover (Wolfe and Summerlin 1989; Orrock et al. 2004), foraging is reduced when moon illumination is high (Wolfe and Summerlin 1989; Orrock et al. 2004), and foraging is greater on nights with precipitation (Orrock et al. 2004). Previous work also suggests that *P. polionotus* responds to at least one direct predator cue (predator urine), although the response to urine may depend upon the duration and distribution of urine application (Orrock et al. 2004). Because *P. polionotus* has the same habitat preferences as *S. invicta*, both are active at similar times (Porter and Tschinkel 1987; Cothran et al. 1991; Vinson 1997), and quantifying risk-mediated shifts in foraging is possible with *P. polionotus* (Orrock et al. 2004), this system is suitable for determining how rodents balance potential interactions with *S. invicta* (i.e., competition or predation) with other risks encountered while foraging.

Our objectives were to: (1) determine how the presence of *S. invicta* affects foraging by *P. polionotus*, (2) determine if the presence of *S. invicta* outweighs, or interacts with, direct cues of predation risk (carnivore urine) and indirect cues of predation risk (cover, moonlight, and precipitation), i.e. is the presence of *S. invicta* sufficient to make rodents reduce foraging under situations where foraging would otherwise be greatest, such as beneath vegetative cover?

Materials and methods

Study location and design

Our study was conducted from 12 July to 1 August 2001 in a 20-ha clearcut at the Savannah River Site, a National Environmental Research Park (NERP) near Aiken, S.C., United States. The field was planted with longleaf pine (*Pinus palustris*) seedlings in 1998, and was also characterized by early-successional plants such as pokeweed (*Phytolacca americana*), partridge pea (*Chamaecrista fasciculata*), *Lespedeza* spp., and blackberry (*Rubus* spp.).

To determine the effects of *S. invicta* and indicators of predation risk on foraging by *P. polionotus*, we used foraging trays with a known amount of millet seeds thoroughly mixed with sand (Brown 1988). As rodents consume the millet seeds, diminishing returns are realized (Morris and Davidson 2000) until the energy gained from continued foraging is balanced by the costs of continued foraging, e.g. predation risk (Brown 1988). The amount of seeds left in a seed tray when the rodent reaches this threshold is called the giving-up density (GUD), which represents a quantitative measure of foraging cost (Brown 1988) when foragers experience diminishing returns and use a fixed quitting-harvest rate or a fixed-time foraging strategy (as Morris and Davidson 2000). Although we did not test whether *P. polionotus* experiences diminishing returns while foraging, studies with similar *Peromyscus* spp. (*P. maniculatus* and *P. leucopus*) have found that the diminishing returns are experienced in the presence (Holtcamp et al. 1997) and absence (Holtcamp et al. 1997; Morris and Davidson 2000) of *S. invicta*. Similarly, rodents have been found to use fixed quitting harvest rate strategies, but may also use fixed-time foraging strategies (Morris and Davidson 2000). With these assumptions, giving-up density is a function of predation risk, metabolic costs of foraging, and missed-opportunity costs (Brown 1988), e.g. foraging rodents may miss the opportunity to mate. By pairing foraging trays within close proximity, it can be assumed that all metabolic foraging costs and missed-opportunity costs are the same, such that differences in giving-up density represent perceived changes in risk of competition or predation among the two foraging trays. Giving-up density has been successfully used to assess factors that affect foraging by rodents (e.g., Kotler et al. 1991; Holtcamp et al. 1997; Thorson et al. 1998; Morris and Davidson 2000), including *P. polionotus* (Orrock et al. 2004). Although not technically a density, we measure GUD as the proportion of seeds remaining in each foraging tray to provide information regarding relative changes caused by *S. invicta*, and facilitate comparison with other studies (Orrock et al. 2004); use of seed mass does not change our findings.

We established nine foraging sites throughout the study area, separated by at least 40 m (radius of average *P. polionotus* home-range is 21 m; Cothran et al. 1991). Each site consisted of two foraging trays. One tray was sheltered, positioned under vegetative cover (e.g., a small tree or shrub). A corresponding tray was exposed, placed outside of vegetative cover, <1 m from the sheltered tray. Each tray was an 11×27×27-cm plastic storage container filled with 1 l sand. A 4-cm-diameter hole was drilled in two adjacent sides. Each tray was filled with a constant volume (4.9 ml) of millet seeds (2.6 g ±0.1 SE, *n* =40 samples) and had a tight-fitting lid that prohibited foraging by avian granivores.

We used predator urine as a direct cue of predation risk (Nolte et al. 1994; Orrock et al. 2004). At each of the nine sites, we applied 12 drops of one of six treatments (urine of bobcat, *Lynx rufus*, ocelot, *Leopardus pardalis*, coyote, *Canis latrans*, red fox, *Vulpes vulpes*, white-tailed deer, *Odocoileus virginianus*, or water) each day using a scent dispenser attached to a wire flag placed 4–5 cm from the opening of each foraging tray (sheltered and exposed). Scent dispensers consisted of a cotton ball within a plastic 35-mm photographic film container with V-shaped slots cut into two sides to allow airflow. In addition to the four types of predator urine, urine of *O. virginianus* was used as a urine control, and water was used as a non-urine control. We obtained *C. latrans*, *V. vulpes*, *L. rufus*, and *O. virginianus* urine from commercial suppliers (Buckeye Scent Company, Ansonia, Ohio and Leg Up Enterprises, Bangor, Me.,

United States). Urine of *L. pardalis* was obtained from an adult male ocelot housed at Big Cat Rescue, Tampa, Fla., United States.

Each day, we visited all trays, inspecting them for signs of foraging activity (e.g., fecal pellets, tracks, seed hulls) and for the presence of *S. invicta*. The presence of *S. invicta* was evident because the ants could not climb out of the tray once burdened with the weight of a millet seed. As such, seed removal by *S. invicta* was negligible, and trays where *S. invicta* was present were generally inundated: mean number of *S. invicta* in a subsample of 22 observations was 23.9 ± 3.7 SE. Seeds were sieved from the sand, and trays were recharged with new seeds that were thoroughly mixed into the sand. Old scent dispensers were removed and replaced with new scent dispensers with a different scent as dictated by a Latin square treatment design. To determine GUD, seed samples were cleaned of hulls and debris, dried at 60°C for 5 h, then weighed.

At least 5 days prior to beginning urine treatments, trays were established to allow rodents to become accustomed to foraging within them (Morris and Davidson 2000). Treatments were applied to three sites (six trays) from 12 to 24 July 2001. On 27 July, observations at one site were discontinued due to technical difficulties, six more sites were added to the experiment, and another round of treatments was applied until 1 August 2001. Between the two rounds of the experiment, we monitored trays each day but applied no scent treatments. Our design is slightly unbalanced because a few observations were affected by animal disturbance and heavy rains.

During the course of the study, *S. invicta* was the primary ant species observed near or within trays, verified by collection and identification of ants from each foraging site. The proportion of ants that were *S. invicta* in a subsample of 169 ants taken from foraging trays was 0.94 ± 0.04 SE. The remaining ants were a native fire ant species, *S. geminata*, which are also likely to compete with *P. polionotus* because they also consume seeds (Ready and Vinson 1995) and sting (Vinson 1997). To be sure that only *P. polionotus* was foraging in the trays, we sampled our study area using Sherman Live Traps (Sherman Traps, Tallahassee, Fla., United States) from 15 to 18 May and from 8 to 14 August. *Peromyscus polionotus* was the only species (13 individuals) captured during 360 trap-nights of sampling effort.

Data analysis

Our design represents a split-plot (Littell et al. 2002). The large experimental unit was the site, where different urine treatments were randomly applied to each site each day in a Latin square design. Our design blocks for temporal variation due to day, as well as for

repeated measures taken on each site (a cross-over design; Littell et al. 2002). The smaller experimental unit was the foraging trays themselves: one tray sheltered beneath vegetation and a corresponding exposed tray outside of vegetative cover <1 m away. Moonlight (proportion of the moon illuminated) was quantified each day with data from the US Naval Observatory in Washington, D.C. Additionally, days were classified by whether or not precipitation occurred during nighttime hours (when *P. polionotus* is active) at a rain station 1.5 km from our study site.

We used a mixed-model analysis of covariance (ANCOVA; Littell et al. 2002), with day and site as random effects, the presence of *S. invicta*, predator scent and tray location (sheltered or exposed), and precipitation as fixed effects, and moon illumination as a covariate. We performed our analyses using SAS Proc Mixed (SAS Institute 2000), using the Kenward-Rogers approximation to determine appropriate denominator degrees of freedom (Littell et al. 2002). We evaluated two- and three-way interactions between moonlight, microhabitat, precipitation, and ant presence. Interactions were not included in the final model unless they were marginally significant ($P < 0.15$). The GUD (proportion of seeds removed) was arcsine square-root transformed prior to analysis to improve normality.

Results

We examined 173 observations collected over 19 days. On average, *S. invicta* was present during $8.75 (\pm 2.84)$ SE observations at four of the nine sites we examined (i.e., 35 total observations with *S. invicta*). The bulk of our observations (65%) were from the four sites where *S. invicta* occurred, although the qualitative outcome of our statistical tests did not differ if only sites where *S. invicta* occurred were used. As such, we retained all of our observations to provide the greatest statistical power. At sites where *S. invicta* occurred in foraging trays, ant distribution was independent of microhabitat ($\chi^2 = 0.30$, $df = 1$, $P = 0.58$, $n = 113$) and precipitation ($\chi^2 = 0.32$, $df = 1$, $P = 0.57$, $n = 113$).

The presence of *S. invicta* led to significant shifts in seed removal by *P. polionotus* (Table 1). Averaged across microhabitat and precipitation, *P. polionotus* removed 47.7% of seeds ($\pm 6.0\%$ SE) when *S. invicta* was absent

Table 1 Mixed-model analysis of covariance (ANCOVA) examining the effect of *S. invicta* presence, predator urine, and indirect indicators of predation risk (sheltered or exposed microhabitat, moon illumination, presence of precipitation) on the giving-up density (GUD) of *Peromyscus polionotus*. GUD was measured by the proportion of seeds remaining in a foraging tray, and was arcsine

square-root transformed. Denominator degrees of freedom (DDF) were determined using the Kenward-Roger approximation (Littell et al. 2002). The interaction is dissected into linear contrasts to examine the effect of *Solenopsis invicta* presence under different levels of microhabitat and precipitation

Effect	NDF, DDF	F-ratio	P
Urine	5, 57.9	1.61	0.17
Microhabitat	1, 14.8	1.52	0.23
Precipitation	1, 16	15.44	<0.01
<i>S. invicta</i> presence	1, 148	11.56	<0.01
Moon illumination	1, 14.8	4.44	0.05
Microhabitat \times precipitation \times <i>S. invicta</i>			
Sheltered vs exposed, rain, <i>S. invicta</i> present	1, 109	1.54	0.22
Sheltered vs exposed, rain, <i>S. invicta</i> absent	1, 43.8	7.35	<0.01
Sheltered vs exposed, no rain, <i>S. invicta</i> present	1, 49.6	3.12	0.08
Sheltered vs exposed, no rain, <i>S. invicta</i> absent	1, 26.1	5.35	0.03

and removed 30.0% of seeds ($\pm 7.2\%$ SE) when *S. invicta* was present. Although the presence of *S. invicta* always led to reduced seed removal (Table 1), the presence of ants also interacted with microhabitat and precipitation (3-way interaction, $F_{4,87.7} = 3.61$, $P < 0.01$; Fig. 1). To focus on ant-related shifts in foraging behavior, these interactions were dissected into linear contrasts (Table 1). In the absence of *S. invicta*, *P. polionotus* removed more seeds from sheltered than exposed trays, regardless of rainfall (Table 1). When *S. invicta* was present, foraging between sheltered and exposed trays depended upon precipitation. On rainless nights when *S. invicta* was present, there was a trend of greater seed removal from exposed trays ($P = 0.08$; Table 1, Fig. 1). On rainy nights when *S. invicta* was present, there was no difference in seed removal between sheltered and exposed trays (Table 1, Fig. 1). Precipitation generally led to greater seed removal (Table 1), although rainfall had the least effect on seed removal from uncovered trays when *S. invicta* was present (linear contrast, $F_{1,43.9} = 2.95$, $P = 0.09$; Fig. 1). In agreement with other recent work at the same study site (Orrock et al. 2004), *P. polionotus* did not respond to predator urine (Table 1; Fig. 1), and seed removal by *P. polionotus* increased with decreasing moon illumination (coefficient $= -0.17$; Table 1).

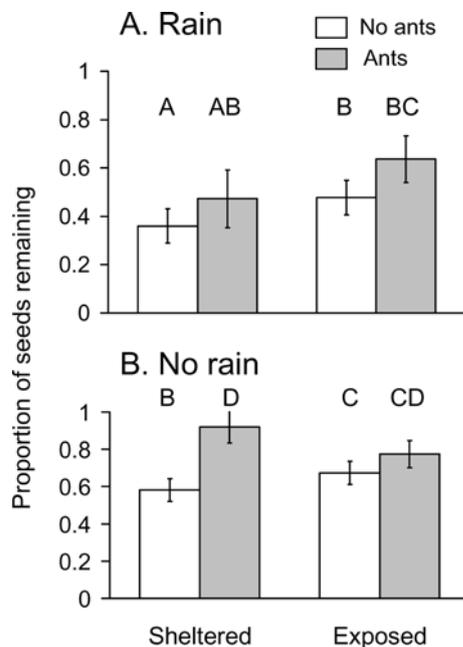


Fig. 1 The mean proportion of seeds remaining in foraging trays after visitation by *Peromyscus polionotus* when fire ants, *Solenopsis invicta*, were absent (open bar) and present (filled bar) on nights where **a** rain occurred and **b** no rain occurred. Trays were either positioned beneath vegetative cover (sheltered), or placed < 1 m away outside of vegetative cover (exposed). Different letters indicate means that are significantly different ($P < 0.05$ using sequential Bonferroni correction; Quinn and Keough 2002). Error bars represent \pm SE, estimated as “broad sense” standard errors (Littell et al. 2002). Arcsin square-root transformed values are used in the analysis, and non-transformed values are presented

Discussion

The presence of *S. invicta* reduced seed removal by *P. polionotus* (Table 1, Fig. 1). Importantly, the presence of *S. invicta* was capable of reducing foraging in previously high-quality microhabitats to levels equal to, or less than, low-quality microhabitats (Fig. 1). That is, based upon differences in seed removal in the presence of *S. invicta*, *P. polionotus* foraging was more sensitive to interactions with *S. invicta* than to risks posed by foraging in exposed versus sheltered microhabitats, and this effect was particularly evident on nights with no precipitation (Fig. 1). Similarly, the presence of *S. invicta* could affect previously safe foraging times; precipitation always increased foraging in ant-free trays, but precipitation had less effect on foraging in exposed trays when *S. invicta* was present (Fig. 1). Interactions among precipitation, microhabitat, and the presence of *S. invicta* suggest that *P. polionotus* assesses tradeoffs among multiple indicators of risk, including the risk of interaction with *S. invicta* (Table 1, Fig. 1). Moreover, our results demonstrate that arthropods are capable of eliciting shifts in rodent foraging similar to those documented for vertebrate competitors and predators (Abramsky et al. 1998).

The response to *S. invicta* may be the result of *P. polionotus* balancing the costs of an interaction with the relative degree of information provided by each cue (Stephens and Krebs 1986). For example, although the cost of an interaction with a predator is likely to be high, cues such as moonlight, precipitation, microhabitat, and predator urine do not provide perfect information (e.g., foraging in exposed microhabitats or in the presence of predator urine does not always result in death; Stephens and Krebs 1986; Blumstein 1996). When *S. invicta* is present, *P. polionotus* may be more certain that competition, and possibly death, will occur, compared to the other indirect and direct cues of predation risk we manipulated. Seed removal by *P. polionotus* when *S. invicta* was absent supported trends found in other studies of rodent foraging: seed removal was greater in sheltered microhabitats (e.g., Kotler et al. 1991; Thorson et al. 1998; Orrock et al. 2004), greater on nights with precipitation (Orrock et al. 2004), greater on nights with little moon illumination (Wolfe and Summerlin 1989; Kotler et al. 1991; Orrock et al. 2004), and unrelated to the short-term presence of predator urine (Orrock et al. 2004).

Our results support other evidence that *S. invicta* can affect rodent behavior (Holtcamp et al. 1997). In a laboratory setting with rich and poor foraging patches, Holtcamp et al. (1997) found that deer mice, *P. maniculatus*, reduced within-patch handling time when *S. invicta* was present. They suggest that *P. maniculatus* was a more efficient forager in the presence of *S. invicta*, and conclude that efficiency was increased because mice biased their foraging efforts towards rich patches (rich patches had 2.5 times more seeds than poor patches) when *S. invicta* was present. In their study, *P. maniculatus* escaped *S. invicta* by spending less time in each seed tray

and leaving the seed tray to consume seeds in ant-free areas (Holtcamp et al. 1997).

Similarly, the interaction between precipitation, microhabitat, and *S. invicta* suggests different foraging strategies in sheltered vs exposed trays may affect how *P. polionotus* responds to *S. invicta*. For example, on rainless nights when *S. invicta* was present, there was a trend of greater seed removal from exposed trays (Fig. 1). This pattern could arise if mice remain within sheltered trays to consume collected seeds, but choose to remove seeds from exposed trays and consume them under protective cover (as suggested by piles of millet hulls found in the vicinity of exposed trays). Such a difference in foraging behavior would lead to reduced interaction with *S. invicta* in exposed trays. That is, although *S. invicta* occurrence did not differ between sheltered and exposed trays, *P. polionotus* may have spent less time consuming seeds within these trays, analogous to *P. maniculatus* that removed seeds from ant-laden patches for consumption in an ant-free area (Holtcamp et al. 1997).

Foraging trends from nights with precipitation are also in agreement with a foraging strategy whereby mice forage from exposed microhabitats and consume seeds elsewhere (Fig. 1), but forage and consume seeds within sheltered tray microhabitats, potentially experiencing heavy competition with *S. invicta*. Precipitation may reduce the impact of *S. invicta* on *P. polionotus* because rain reduces ant foraging by 40% (Porter and Tschinkel 1987). Rainfall may also interfere with the ability of ants to recruit nestmates by plugging subterranean tunnels and interfering with pheromones (Porter and Tschinkel 1987), potentially reducing the competitive strength of *S. invicta*. As such, if rainfall affects the relationship between *S. invicta* and *P. polionotus*, rain would be expected to have the greatest impact on foraging in sheltered trays when ants were present, but not change the value of exposed ant-laden trays, in agreement with our observations (compare frames in Fig. 1). Activity on rainy nights may not be clearly reflected in patterns of *S. invicta* within foraging trays because these ants may have entered (and remained within) trays before or after precipitation.

The ability of *P. polionotus* to recognize *S. invicta* and shift foraging behavior may minimize competitive and otherwise negative interactions. Future work should focus on how habitat use may allow *P. polionotus* to reconcile reduced foraging when *S. invicta* is abundant or *S. invicta* activity is high. For example, *P. polionotus* may construct burrows in areas where *S. invicta* activity is lower (as found for *B. taylori*; Killion et al. 1995) or forage most intensively during early morning hours when low soil temperatures may reduce *S. invicta* activity (Porter and Tschinkel 1987). Similarly, *P. polionotus* foraging may exhibit seasonal shifts in areas of high *S. invicta* density as found for transient *B. taylori* that avoided areas of high *S. invicta* density in the summer (Smith et al. 1990). Such temporal and seasonal shifts in rodent behavior have been observed in response to other competitors (Abramsky et al. 2001) and predators (Bouskila 1995).

Our work provides evidence that *S. invicta* can affect foraging by *P. polionotus*, and that this effect depends upon the microhabitat of the foraging area (sheltered or exposed) and climatic conditions during the foraging event, i.e. precipitation. From the perspective of *P. polionotus*, *S. invicta* may affect foraging decisions and reduce the time spent foraging in otherwise low-risk microhabitats and during low-risk periods. Because *P. polionotus* can affect the distribution of plants via seed predation (Orrock et al. 2003), ant-mediated shifts in rodent foraging could have indirect effects on the plant community (Brown and Heske 1990).

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References

- Abramsky Z, Rosenzweig ML, Subach A (1998) Do gerbils care more about competition or predation? *Oikos* 83:75–84
- Abramsky Z, Rosenzweig ML, Subach A (2001) The costs of interspecific competition in two gerbil species. *J Anim Ecol* 70:561–567
- Blumstein DT (1996) Assessment and decision making in animals: a mechanistic model underlying behavioral flexibility can prevent ambiguity. *Oikos* 77:569–576
- Bouskila A (1995) Interactions between predation risk and competition: a field study of kangaroo rats and snakes. *Ecology* 76:165–178
- Brown JH, Heske EJ (1990) Control of a desert-grassland transition by a keystone rodent guild. *Science* 250:1705–1707
- Brown JS (1988) Patch use as an indicator of habitat preference, predation risk, and competition. *Behav Ecol Sociobiol* 22:37–47
- Cothran EG, Smith MH, Wolff JO, Gentry JB (1991) Mammals of the savannah river site, SRO-NERP-21. Savannah River Site, Aiken, S.C.
- Ferris DK, Killion MJ, Ferris KP, Grant WE, Vinson SB (1998) Influence of relative abundance of red imported fire ants (*Solenopsis invicta*) on small mammal captures. *Southwest Nat* 43:97–100
- Holtcamp WN, Grant WE, Vinson SB (1997) Patch use under predation hazard: effect of the red imported fire ant on deer mouse foraging behavior. *Ecology* 78:308–317
- Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ (2002) The causes and consequences of ant invasions. *Annu Rev Ecol Syst* 33:181–233
- Killion MJ, Grant WE (1993) Scale effects in assessing the impact of imported fire ants on small mammals. *Southwest Nat* 38:393–396

- Killion MJ, Grant WE, Vinson SB (1995) Response of *Baiomys taylori* to changes in density of imported fire ants. *J Mamm* 76:141–147
- Kotler BP, Brown JS, Hasson O (1991) Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* 72:2249–2260
- Kotler BP, Blaustein L, Brown JS (1992) Predator facilitation: the combined effect of snakes and owls on the foraging behavior of gerbils. *Ann Zool Fenn* 29:199–206
- Lechner KA, Ribble DO (1996) Behavioral interactions between red imported fire ants (*Solenopsis invicta*) and three rodent species of south Texas. *Southwest Nat* 41:123–128
- Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48:25–34
- Littell RC, Stroup WW, Freund RJ (2002) SAS for linear models. SAS Institute, Cary, N.C.
- Masser MP, Grant WE (1986) Fire ant-induced trap mortality of small mammals in east-central Texas. *Southwest Nat* 31:540–542
- Morris DW, Davidson DL (2000) Optimally foraging mice match patch use with habitat differences in fitness. *Ecology* 81:2061–2066
- Nolte DL, Mason JR, Eppel G, Aronov E, Campbell DL (1994) Why are predator urines aversive to prey? *J Chem Ecol* 20:1505–1516
- Orrock JL, Danielson BJ, Burns MJ, Levey DJ (2003) Spatial ecology of predator-prey interactions: corridors and patch shape influence seed predation. *Ecology* 84:2520–2526
- Orrock JL, Danielson BJ, Brinkerhoff RJ (2004) Rodent foraging is affected by indirect, but not direct, cues of predation risk. *Behav Ecol* 15:433–437
- Quinn, GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge
- Porter SD, Tschinkel WR (1987) Foraging in *Solenopsis invicta* (Hymenoptera: Formicidae): effects of weather and season. *Environ Entomol* 16:802–808
- Ready CC, Vinson SB (1995) Seed selection by the red imported fire ant (Hymenoptera: Formicidae) in the laboratory. *Environ Entomol* 24:1422–1431
- SAS Institute (2000) SAS user's guide. Version 8.1. SAS Institute, Cary, N.C.
- Schmitz OJ, Beckerman AP, O'Brien KM (1997) Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78:1388–1399
- Smith TS, Smith SA, Schmidly DJ (1990) Impact of fire ant (*Solenopsis invicta*) density on northern pygmy mice (*Baiomys taylori*). *Southwest Nat* 35:158–162
- Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton, N.J.
- Thorson J, Morgan R, Brown J, Norman J (1998) Direct and indirect cues of predatory risk and patch use by fox squirrels and thirteen-lined ground squirrels. *Behav Ecol* 9:151–157
- Vinson SB (1997) Invasion of the red imported fire ant (Hymenoptera: Formicidae): spread, biology, and impact. *Am Entomol* 43:23–39
- Wolfe JL, Summerlin CT (1989) The influence of lunar light on nocturnal activity of the old-field mouse. *Anim Behav* 37:410–414