

Rodent foraging is affected by indirect, but not by direct, cues of predation risk

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We used foraging trays to determine whether oldfield mice, *Peromyscus polionotus*, altered foraging in response to direct cues of predation risk (urine of native and nonnative predators) and indirect cues of predation risk (foraging microhabitat, precipitation, and moon illumination). The proportion of seeds remaining in each tray (a measure of the giving-up density [GUD]) was used to measure risk perceived by mice. Mice did not alter their GUD when presented with cues of native predators (bobcats, *Lynx rufus*, and red foxes, *Vulpes vulpes*), recently introduced predators (coyotes, *Canis latrans*), nonnative predators (ocelots, *Leopardus pardalis*), a native herbivore (white-tailed deer, *Odocoileus virginianus*), or a water control. Rather, GUD was related to microhabitat: rodents removed more seeds from foraging trays sheltered beneath vegetative cover compared with exposed trays outside of cover. Rodents also removed more seeds during nights with precipitation and when moon illumination was low. Our results suggest that *P. polionotus* used indirect cues rather than direct cues to assess risk of vertebrate predation. Indirect cues may be more reliable than are direct scent cues for estimating risk from multiple vertebrate predators that present the most risk in open environments. *Key words*: foraging, giving-up densities, *Peromyscus polionotus*, predator recognition; prey behavior; risk assessment; Savannah River Site. [*Behav Ecol* 15:433–437 (2004)]

Antipredator behavior can affect the fitness of individuals (Curio, 1993; Lima, 1998a,b; Lima and Dill, 1990) and the dynamics of populations (Brown et al., 1999; Lima, 1998a). Although evidence suggests that prey can detect cues of different predators and respond accordingly (see Curio, 1993; Kats and Dill, 1997; Kotler et al., 1991; Lima, 1998b), little is known about whether predator-specific risk assessment and response are common among prey, or if prey use simpler “rules of thumb” to avoid risk (Bouskila and Blumstein, 1992). Understanding how prey assess and respond to risk may provide insight into how predation risk affects the structure of ecological communities (Brown et al., 1999; Kotler, 1984; Schmitz et al., 1997), including decimation of prey by introduced predators (Williamson, 1996) and the reintroduction of rare species (Blumstein et al., 2000; Griffin et al., 2000).

Rodents are prey for avian, reptilian, and mammalian predators. Evidence suggests that rodents alter their foraging in risky situations. For example, rodents preferentially forage in sheltered microhabitats (often under vegetative cover), where the risk of avian predation is lower (see Kotler et al., 1991). Foraging may be greater when precipitation or lack of moonlight reduces the ability of vertebrate predators to detect and capture rodents (King, 1968; Kotler et al., 1991). Rodents may also avoid forest edges, where vertebrate predation risk is greater (Morris and Davidson, 2000), or forage more intensively close to refuges and escape routes (Brown and Morgan, 1995; Thorson et al., 1998). The robustness of this pattern suggests that mice alter their foraging in different microhabitats by using indirect cues (dangerous microhabitats) rather than direct cues (a cue produced by the predator, such as urine or sound). As such, mice may use a simple rule of thumb to moderate antipredator behavior: avoid dangerous places.

However, whether a place is dangerous may depend upon the presence of a particular predator. Foraging by oldfield mice, *Peromyscus polionotus*, was reduced in experimental patches where bobcat (*Lynx rufus*) urine was added compared with patches with no urine addition (Brinkerhoff RJ, unpublished data). Rodents are at risk of avian predation in exposed microhabitats but are more susceptible to predation by snakes in sheltered microhabitats (Bouskila, 1995; Kotler et al., 1991; Kotler et al., 1993). At least one species of desert rodent can discriminate among avian predators and alters its behavior accordingly (Kotler et al., 1991). Similarly, fox squirrels (*Sciurus niger*) and 13-lined ground squirrels (*Spermophilus tridecemlineatus*) alter foraging in the presence of a plastic owl model but not in the presence of red fox (*Vulpes vulpes*) urine (Thorson et al., 1998). Rodents may respond to predator urine in a general fashion, using sulfur compounds as an indicator of the amount of meat in a predator’s diet (Nolte et al., 1994). Alternatively, rodents may exhibit predator-specific responses, behaving differently in the presence of odors from different terrestrial predators (Jedrzejewski et al., 1993).

Our first objective was to examine the importance of indirect cues of predation risk (e.g., exposed or sheltered microhabitats) compared with direct cues (predator urine). Our second objective was to examine whether rodents recognize specific terrestrial predator types (e.g., discriminating between bobcats and red foxes), which would be advantageous if predators differ in their impact on rodent fitness. In addition to using urine of native predators, we also tested urine of predators that have recently (within 30 years) become sympatric with rodents and those that have never been sympatric with rodents.

Prey may respond to predation risk by exhibiting a short-term reduction in foraging that can only be sustained for a short time before other constraints (e.g., hunger) make it necessary to resume foraging activity (Lima and Bednekoff, 1999). As such, short-lived field studies that manipulate risk may overestimate the perception of risk by prey and may not be indicative of prey responses over more reasonable time spans, in which prey must balance predation risk with other activities

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(e.g., food and mate acquisition; Lima and Bednekoff, 1999). To examine this possibility, our third objective was to determine if mice became less responsive to our experimentally manipulated predator cues as the experiment progressed. If so, this should be evident as a significant time and a significant predator cue effect if mice respond to all predator cues, or a significant time by predator cue interaction if mice respond to some predator cues.

METHODS

Study location and study species

Our study was conducted from 19 May–24 July 2001 in an early-successional field at the Savannah River Site, a National Environmental Research Park (NERP) near Aiken, South Carolina. The field was planted with Longleaf Pine (*Pinus palustris*) in 1998 and also contained early-successional plants such as pokeweed (*Phytolacca americana*), partridge pea (*Chamaecrista fasciculata*), *Lespedeza* spp., and blackberry (*Rubus* spp.). The study area represents high-quality habitat for the oldfield mouse, *P. polionotus* (Cothran et al., 1991). *P. polionotus* has a limited geographic range that extends along coastal regions from Florida north to central South Carolina, and west to portions of Alabama (Hall, 1981; King, 1968).

Historically, the range of *P. polionotus* has overlapped with that of bobcats, *L. rufus*, and red foxes, *V. vulpes* (King, 1968; Larivière and Pasitschniak-Arts, 1996; Larivière and Walton, 1997). Coyotes, *C. latrans*, recently expanded their geographic range and were first documented at our study area in 1989 (Cothran et al., 1991). Ocelots, *Leopardus pardalis*, are predators that have never been present in the study area (Hall, 1981).

All of these predators are known to prey upon mice, although rodents are more frequent in the diet of *V. vulpes* compared with *L. rufus* and *C. latrans*, which both prey more frequently upon rabbits and larger rodents (Bekoff, 1977; Larivière and Pasitschniak-Arts, 1996; Larivière and Walton, 1997; Major and Sherburne, 1987). Based upon predator diet, if *P. polionotus* can discriminate among cues of all predator types, foraging activity should be ranked (from least to greatest): *V. vulpes* < *L. rufus* ≤ *L. pardalis* < *C. latrans*. However, *V. vulpes* may not be locally abundant in the study area, whereas *C. latrans* populations are probably still rising (Weston, 2002). Because local density and activity of predators are not known and predator efficiency and diet are unlikely to be constant in time, our prediction is necessarily subjective.

Experimental design

We used predator urine as a cue to suggest the presence of each predator type. Olfactory predator cues are known to affect the behavior of a variety of organisms (Kats and Dill, 1997), including *P. polionotus* (Brinkerhoff RJ, unpublished data), *Peromyscus* spp. (Nolte et al., 1994), and other rodents (see Jedrzejewski et al., 1993; Kats and Dill, 1997; Sullivan et al., 1988; Swihart, 1991). In addition to four types of predator urine, urine of white-tailed deer, *Odocoileus virginianus*, was used as a urine control, and water was used as a nonurine control. We obtained *C. latrans*, *V. vulpes*, *L. rufus*, and *O. virginianus* urine from commercial suppliers (Buckeye Scent Company and Leg Up Enterprises). Urine of *L. pardalis* was obtained from an adult male ocelot housed at Wildlife on Easy Street.

To measure the risk perceived by *P. polionotus* while foraging, we used foraging trays with a known amount of seeds thoroughly mixed with a homogenous substrate (sand). As a foraging rodent depletes the seeds, diminishing returns are realized (Brown, 1988; Morris and Davidson, 2000). At some

point the benefits of continued foraging are outweighed by the costs, including the risk of predation (Brown, 1988). This threshold, called the giving-up density (GUD; Brown, 1988) represents a quantitative measure of perceived predation risk if everything else experienced by the forager among treatments can be assumed to be equal (Brown, 1988) and has been used to quantify predation risk experienced by rodents (see Bouskila, 1995; Herman and Valone, 2000; Kotler et al., 1991; Morris and Davidson, 2000; Thorson et al., 1998).

Within the old field, we established nine sites, each consisting of two foraging trays located in a different microhabitat. One tray was sheltered, positioned under vegetative cover (e.g., a shrub or small tree). The corresponding tray was exposed, placed outside of cover, less than 1 m away. Each tray was a 27 × 27 × 11-cm plastic storage container filled with 1 l of sand. A 2.5-cm-diameter hole was drilled in each of two adjacent sides. A constant volume of millet seeds representing 2.62 g ± 0.08 SE ($N = 40$ samples) was added to each tray. GUD was determined by weighing remaining seeds after removal of seed hulls and debris and is expressed as the proportion of seeds remaining. Seeds were dried for 5 h at 60°C before weighing.

At each site, we applied 12 drops of one of six treatments (water or urine of *L. rufus*, *L. pardalis*, *C. latrans*, *V. vulpes*, or *O. virginianus*) each day by using a scent dispenser attached to a wire pin flag 4–5 cm from the openings of each seed tray in each microhabitat (sheltered and exposed). Scent dispensers consisted of a cotton ball within a plastic film can with V-shaped slots cut into two sides to allow airflow. Each day, we visited all trays and recorded signs of foraging activity (e.g., fecal pellets, tracks, seed hulls). Seeds were sieved from each tray, and the tray was charged with new seeds, which were thoroughly mixed into the sand. Old scent dispensers were removed and replaced with new scent dispensers, with a different scent as dictated by the treatment design.

At least 3 days before beginning urine treatments, trays were established and rodents allowed to forage in treatment-free trays to become acclimated (Morris and Davidson, 2000). A complete round of treatments was applied to six sites (12 trays) from 19–24 May 2001. We added three more sites to the experiment and applied treatments at all trays from 12–24 July 2001. Between the two rounds of the experiment, we monitored trays each day but applied no scent treatments.

Data analysis

Our design represents a split-plot design (Littell et al., 1996). Our data were slightly unbalanced because sites were removed from the study if foraging activity ceased or trays became occupied by fire ants, *Solenopsis* spp. (mean number of complete rounds of urine treatments per site was 2.4 ± 0.3 SE). The large experimental unit was the site, where different treatments were applied to each site each day in a Latin square design. Our design blocks for temporal variation owing to day, as well as for repeated measures taken on each site (a cross-over design; Littell et al., 1996). The smaller experimental unit was the foraging trays themselves. At each site, one tray was positioned under cover, and the corresponding tray was not under cover. Moonlight (proportion of the moon illuminated) was quantified each day with data from the US Naval Observatory in Washington, DC, and the number of days that the experiment had been conducted at a site was measured as a covariate for each site. Days were also classified by the occurrence of precipitation during nighttime hours at a rain station 1.5 km from our study site.

Our mixed-model ANOVA (Littell et al., 1996) specified time and site as random effects, predator scent and tray location (covered or exposed) as fixed effects, precipitation as

a fixed effect, and moon illumination as a covariate. The number of days urine treatments had been run at a tray was a covariate in our model to determine if risk-aversion decreased with time (Lima and Bednekoff, 1999). If a significant urine treatment effect was found, we compared all treatments in a pairwise fashion, using the Tukey-Kramer adjustment for multiple comparisons (SAS, 2000).

We performed retrospective power analysis if we found no significant difference among treatments for the main fixed effects in our model to determine the effect sizes detectable by our design (Thomas, 1997). We calculated the noncentrality parameter for each effect by using the method and formulae of Stroup (2002), and we used the observed variance from our mixed-model analysis (Thomas, 1997). We use a two-tailed type I error rate (α) of 0.05 for calculating power.

We performed our analyses using SAS Proc Mixed (SAS, 2000). The Satterthwaite method (Littell et al., 1996) was used to generate the approximate denominator degrees of freedom owing to the slightly unbalanced nature of our data. We evaluated two- and three-way interactions and did not consider them for inclusion in the final model unless they were marginally significant ($p < .15$; Littell et al., 1996).

RESULTS

We examined 254 foraging observations taken from nine sites over 19 days. Foraging activity was evident in 237 (93%) of the observations and was independent of predator cue ($\chi^2 = 1.06$, 5 df, $p = .96$). Seed removal by *P. polionotus* did not change in response to vertebrate predator cues ($F_{5,97.4} = 0.69$, $p = .63$) (Figure 1). Rather, *P. polionotus* altered foraging based on microhabitat characteristics: rodents removed an average of 64% of seeds in covered trays compared with 55% of seeds in exposed trays ($F_{1,124} = 23.10$, $p < .01$) (Figure 1). Rodents removed an average of 67% of seeds on nights with precipitation compared with 52% of seeds on nights without precipitation ($F_{1,15.8} = 12.99$, $p < .01$) (Figure 1). GUD increased as the proportion of the moon illuminated increased ($F_{1,17.7} = 11.33$, $p < .01$; coefficient = 0.23 ± 0.07 SE). The duration of treatments at a site did not influence GUD ($F_{1,27.8} = .43$, $p = .50$). There were no significant interactions (all p values $> .20$).

We estimated the effect size our study could have detected if the response to urine only occurred to *L. rufus*, namely, as if all other treatments were equal. We use this approach because other research using *L. rufus* urine detected a reduction of seed removal by *P. polionotus* (Brinkerhoff RJ, unpublished data), suggesting that *P. polionotus* was capable of detecting and responding to at least one of the urines we used. This approach is conservative because power increases if a reduction in seed removal of the same magnitude occurs in response to more than one urine type (Quinn and Keough, 2002). Based upon our sample sizes, we were able to detect a 45% change in foraging with 80% power. This is well below the effect of *L. rufus* urine found in our other work (foraging was 81% greater when *L. rufus* urine was not present, paired t test, $t = 4.62$, 2 df, $p = .04$; Brinkerhoff RJ, unpublished data).

To be sure that only *P. polionotus* was foraging in the trays, we sampled our study area using Sherman Live Traps (Sherman Traps). The first trapping session occurred from 15–18 May, and the second session occurred from 8–14 August. *P. polionotus* was the only species captured during these sessions; 13 individuals were captured during 360 trap-nights of sampling.

DISCUSSION

Rather than respond to direct predator-related cues, seed removal by *P. polionotus* differed in response to indirect cues of

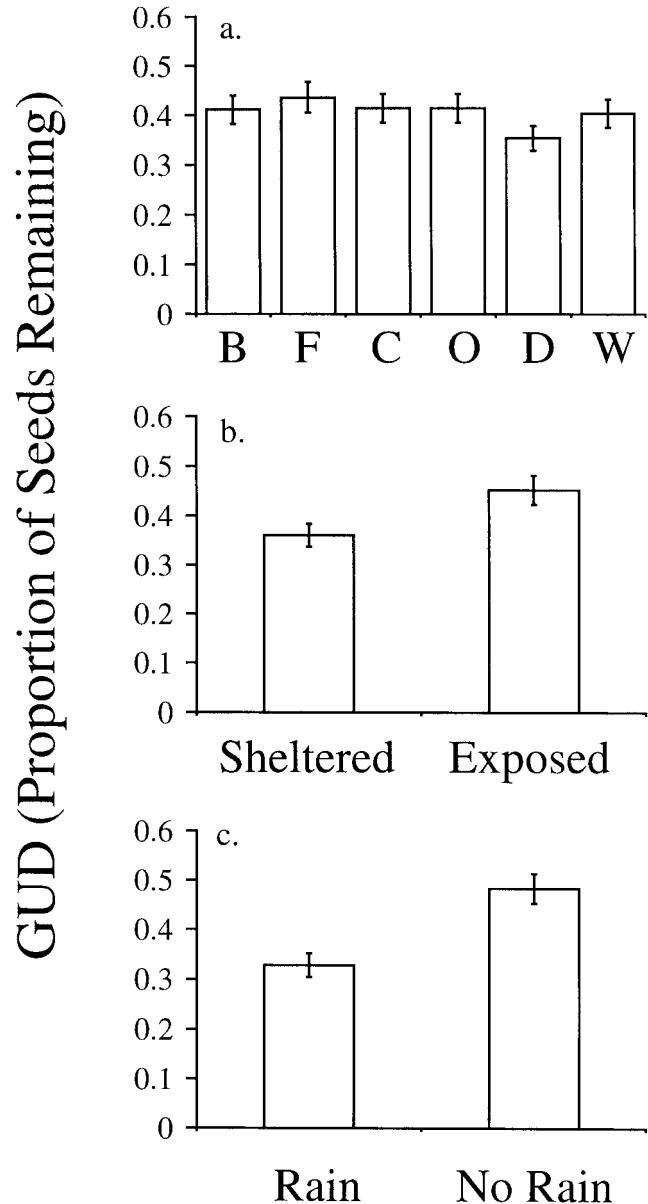


Figure 1

The mean proportion of seeds (\pm SE) left in foraging trays by *Peromyscus polionotus* from 19 May–24 July 2002 at the Savannah River Site. (a) There was no significant difference in the proportion of seeds removed in response to the scent of native predators (B indicates bobcats; F, foxes), recently introduced predators (C, coyotes), nonnative predators (O, ocelots), a native herbivore (D, white-tailed deer), and a control (W, water). (b) *P. polionotus* removed significantly more seeds ($p < .01$) from trays located in microhabitats sheltered beneath vegetative cover (sheltered) rather than adjacent trays less than 1 m away in microhabitats that were not under cover (exposed). (c) More seeds ($p < .01$) were removed from trays during nights with precipitation compared with nights when no precipitation occurred.

predation risk: moon illumination, precipitation, and whether a foraging area was in an exposed or sheltered microhabitat. These cues are likely to be effective because they convey consistent information about risk from multiple predators. For example, many of the predators at our study sites forage in exposed habitats: owls, foxes, bobcats, and coyotes can all be evaded if a rodent is close enough to cover. Thus, indirect cues may be useful integrators of multiple risks; namely, distance

from cover may provide more information about more predators than does the scent cue of a particular predator. Although there was no trend between foraging activity and the duration of the experiment, we cannot evaluate whether risk tolerance increased with the duration of the experiment because *P. polionotus* did not respond to the risk we directly manipulated; namely, there was no significant effect of time and predator scent, and no significant predator scent by time interaction.

There are three potential explanations for the lack of an observed change in GUD in the presence of predator urine. First, *P. polionotus* may have been unable to discriminate among the scents used in the present study, either because *P. polionotus* is incapable of discriminating among scents of predators, deer, and water, or because the scents we used were not representative of the scents of predators and thus elicited no response. There is ample evidence from laboratory and controlled field settings that rodents can discriminate among predator scents (see Herman and Valone, 2000; Jedrzejewski et al., 1993; Kats and Dill, 1997; Parsons and Bondrup-Nielsen, 1996), including *L. rufus* (Swihart, 1991), *V. vulpes* (Dickman, 1992; Rosell, 2001; Sullivan et al., 1988), and *C. latrans* (Nolte et al., 1994). Moreover, in another study, we found that *P. polionotus* removed fewer seeds in experimental landscapes where *L. rufus* urine was applied over a 2-week period (Brinkerhoff RJ, unpublished data). It is also likely that the urine we used was capable of eliciting a response because predator urine was obtained from animals fed a meat-rich diet, and the sulfur-rich compounds present in the urine of carnivorous animals are generally aversive to rodents (Nolte et al., 1994).

A second explanation for the lack of change in GUD in the presence of predator urine is that our analysis lacked the statistical power necessary to detect a biologically meaningful effect size. Our retrospective power analysis suggests that our study had 80% power to detect 45% change in seed removal in response to just one of the six treatments. This change is much smaller than the 81% effect size we noted when *P. polionotus* was exposed to *L. rufus* urine in another experiment (Brinkerhoff RJ, unpublished data). As such, it is not likely that lack of power is responsible for the lack of a urine treatment effect we observed.

A third explanation for the lack of change in GUD in the presence of predator urine is that *P. polionotus* may be able to discriminate among predator scents, but chooses not to alter its foraging behavior. Under this scenario, discrimination is possible, but the payoff of discrimination (the usefulness of the information provided by the cue) may be outweighed by opportunities missed during the act of discrimination (missed-opportunity costs; Brown, 1988). Because discrimination among predator scents is not likely to cost much in terms of time (Jedrzejewski et al., 1993), it seems most likely that predator urine provides low-quality information under the field conditions of our study. This interpretation is in agreement with other evidence that indirect cues are more often used than are scent-based direct cues (Thorson et al., 1998), evidence that responses to direct cues are weak or transient (Herman and Valone, 2000; Parsons and Bondrup-Nielsen, 1996), and studies that support the importance of microhabitat, illumination, and precipitation (see Bowers et al., 1993; King 1968; Kotler et al., 1991; Morris and Davidson, 2000; Thorson et al., 1998; Wolfe and Summerlin, 1989). In addition to reducing predation risk, precipitation may also decrease foraging costs by increasing humidity, making seeds easier for mice to locate (Vander Wall, 1995).

Our findings suggest that the amount of information conveyed by a cue may be dependent upon its cost relative to the quantity and quality of information already at hand (Brown et al., 1999). For example, costs of reproduction may

explain why adult male bank voles respond to predator odors but breeding females do not (Jedrzejewski and Jedrzejewska, 1990). Seasonal shifts in the effectiveness of predator urine cues (Herman and Valone, 2000) provide more support that the relative importance of direct and indirect cues is context dependent. Other considerations, such as predator density, foraging duration, spatial distribution, and whether the presence of one predator type facilitates capture by another predator type, could also affect the relative importance of direct versus indirect cues (Brown et al., 1999). Direct cues may become more important as evidence of predator presence increases (Brown et al., 1999), presumably because continued presence of scent is indicative of a resident, rather than transient, predator. For example, R.J. Brinkerhoff (unpublished data) found that *P. polionotus* did reduce foraging activity in the presence of *L. rufus* urine, but urine was presented for a longer duration than in the present study (2 weeks). It is unclear how this may have impacted our results, because a predator scent was present at each foraging station during 67% of the treatments (four of the six treatments were predator urine), and treatments were applied for 1- and 2-week periods, but the type of urine was changed each day of the study. Future work that examines the importance of cue duration and consistency would be a profitable next step in dissecting the relationship between direct and indirect cues.

In conclusion, our work suggests that indirect cues may be more useful than are direct cues for rodents that are consumed by a variety of predators, probably because indirect cues provide reliable, easily assessed information regarding the risk from multiple predator types (Blumstein et al., 2000). From a conservation perspective, this suggests that native prey may not be affected by nonnative predators if the prey rely upon indirect cues of risk that are effective against many predator types. Our findings suggest that the effectiveness of using predator scents to deter damage by rodents (Rosell, 2001; Sullivan et al., 1988) may depend upon the ecological circumstances under which the predator scent is applied (Swihart, 1991). From an ecological perspective, our work suggests that differences in rodent foraging behavior caused by indirect cues of predation risk may reduce the impact of rodent granivores on seed banks in exposed risky environments, and may affect the structure and composition of rodent communities (Kotler, 1984).

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REFERENCES

- Bekoff M, 1977. *Canis latrans*. Mammal Species 79:1-9.
 Blumstein DT, Daniel JC, Griffin AS, Evans CS, 2000. Insular tammar wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators. Behav Ecol 115:28-535.

- Bouskila A, 1995. Interactions between predation risk and competition: a field study of kangaroo rats and snakes. *Ecology* 76:165–178.
- Bouskila A, Blumstein DT, 1992. Rules of thumb for predation hazard assessment: predictions from a dynamic model. *Am Nat* 139:161–176.
- Bowers MA, Jefferson JL, Kueber MG, 1993. Variation in giving-up densities of foraging chipmunks (*Tamias striatus*) and squirrels (*Sciurus carolinensis*). *Oikos* 66:229–236.
- Brown JS, 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav Ecol Sociobiol* 22:37–47.
- Brown JS, Laundré JW, Gurung M, 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *J Mammal* 80:385–399.
- Brown JS, Morgan RA, 1995. Effects of foraging behavior and spatial scale on diet selectivity: a test with fox squirrels. *Oikos* 74:122–136.
- Cothran EG, Smith MH, Wolff JO, Gentry JB, 1991. Mammals of the Savannah River Site. SRO-NERP-21. Aiken, South Carolina: Savannah River Site.
- Curio E, 1993. Proximate and developmental aspects of antipredator behavior. *Adv Study Behav* 22:135–238.
- Dickman CR, 1992. Predation and habitat shifts in the house mouse, *Mus domesticus*. *Ecology* 73:313–322.
- Griffin AS, Blumstein DT, Evans CS, 2000. Training captive-bred or translocated animals to avoid predators. *Conserv Biol* 14:1317–1326.
- Hall ER, 1981. The mammals of North America. New York: Wiley.
- Herman CS, Valone TJ, 2000. The effect of mammalian predator scent on the foraging behavior of *Dipodomys merriami*. *Oikos* 91:139–145.
- Jedrzejewski W, Jedrzejewska B, 1990. Effect of a predator's visit on the spatial distribution of bank voles: experiment with weasels. *Can J Zool* 68:660–666.
- Jedrzejewski W, Rychlik L, Jedrzejewska B, 1993. Responses of bank voles to odours of seven species of predators: experimental data and their relevance to natural predator-vole relationships. *Oikos* 68:251–257.
- Kats LB, Dill LM, 1997. The scent of death: chemosensory assessment of predation risk by prey animals. *Écoscience* 361–394.
- King, JA, 1968. Biology of *Peromyscus* (Rodentia). Stillwater, Oklahoma: American Society of Mammalogists.
- Kotler BP, 1984. Risk of predation and the structure of desert rodent communities. *Ecology* 65:689–701.
- Kotler BP, Brown JS, Hasson O, 1991. Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* 72:2249–2260.
- Kotler BP, Brown JS, Slotow RH, Goodfriend WL, Strauss M, 1993. The influence of snakes on the foraging behavior of gerbils. *Oikos* 53:145–152.
- Larivière S, Pasitschniak-Arts M, 1996. *Vulpes vulpes*. *Mammal Species* 537:1–11.
- Larivière S, Walton LR, 1997. *Lynx rufus*. *Mammal Species* 563:1–8.
- Lima SL, 1998a. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48:25–34.
- Lima SL, 1998b. Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Adv Study Behav* 27:215–290.
- Lima SL, Bednekoff PA, 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am Nat* 153:649–659.
- Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640.
- Littell RC, Milliken GA, Stroup WW, Wolfinger RD, 1996. SAS system for mixed models. Cary, North Carolina: SAS Institute.
- Major JT, Sherburne JA, 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. *J Wildl Manage* 51:606–616.
- 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.
- Parsons GJ, Bondrup-Nielsen S, 1996. Experimental analysis of behavior of meadow voles (*Microtus pennsylvanicus*) to odours of the short-tailed weasel (*Mustela erminea*). *Écoscience* 3:63–69.
- Quinn GP, Keough MJ, 2002. Experimental design and data analysis for biologists. Cambridge: Cambridge University Press.
- Rosell F, 2001. Effectiveness of predator odors as gray squirrel repellents. *Can J Zool* 79:1719–1723.
- SAS Institute, 2000. SAS user's guide. Version 8.1. Cary, North Carolina: SAS Institute.
- Schmitz OJ, Beckerman AP, O'Brien KM, 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78:1388–1399.
- Stroup WW, 2002. Power analysis based on spatial effects mixed models: a tool for comparing design and analysis strategies in the presence of spatial variability. *J Agric Biol Environ Stat* 7:491–511.
- Sullivan TP, Crump DR, Sullivan DS, 1988. Use of predator odors as repellents to reduce feeding damage by herbivores, III: montane and meadow voles (*Microtus montanus* and *Microtus pennsylvanicus*). *J Chem Ecol* 14:363–377.
- Swihart RK, 1991. Modifying scent-marking behavior to reduce woodchuck damage to fruit trees. *Ecol App* 1:98–103.
- Thomas L, 1997. Retrospective power analysis. *Conserv Biol* 11:276–280.
- Thorson J, Morgan R, Brown J, Norman J, 1998. Direct and indirect cues of predatory risk and patch use by fox squirrels and 13-lined ground squirrels. *Behav Ecol* 9:151–157.
- Vander Wall SB, 1995. Influence of substrate water on the ability of rodents to find buried seeds. *J Mammal* 76:851–856.
- Weston JLM, 2002. Demographics of a protected population of gray foxes (*Urocyon cinereoargenteus*) in South Carolina (PhD dissertation). Athens: University of Georgia.
- Williamson M, 1996. Biological invasions. London: Chapman and Hall.
- Wolfe JL, Summerlin CT, 1989. The influence of lunar light on nocturnal activity of the old-field mouse. *Anim Behav* 37:410–414.