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CORRIDORS AND OLFACTORY PREDATOR CUES AFFECT SMALL MAMMAL BEHAVIOR

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The behavior of prey individuals is influenced by a variety of factors including, but not limited to, habitat configuration, risk of predation, and availability of resources, and these habitat-dependent factors may have interactive effects. We studied the responses of mice to an increase in perceived predation risk in a patchy environment to understand how habitat corridors might affect interactions among species in a fragmented landscape. We used a replicated experiment to investigate corridor-mediated prey responses to predator cues in a network of open habitat patches surrounded by a matrix of planted pine forest. Some of the patches were connected by corridors. We used mark–recapture techniques and foraging trays to monitor the movement, behavior, and abundance of small mammals. Predation threat was manipulated in one-half of the replicates by applying an olfactory predator cue. Corridors synchronized small mammal foraging activity among connected patches. Foraging also was inhibited in the presence of an olfactory predator cue but apparently increased in adjacent connected patches. Small mammal abundance did not change as a result of the predator manipulation and was not influenced by the presence of corridors. This study is among the 1st to indicate combined effects of landscape configuration and predation risk on prey behavior. These changes in prey behavior may, in turn, have cascading effects on community dynamics where corridors and differential predation risk influence movement and patch use.

Key words: corridors, foraging, habitat fragmentation, movement, *Peromyscus*, Savannah River Site

Given the potentially dire consequences that fragmentation poses for species persistence (Fahrig and Merriam 1994; Hanski 1997; Pimm et al. 1995) and the rapid global loss of habitat due to anthropogenic effects (Seabloom et al. 2002), studies of species interactions and community dynamics in fragmented landscapes are crucial to conservation. Wilson and Willis (1975) suggested the use of corridors to mitigate some of the negative effects of habitat fragmentation by allowing continuing immigration to offset local extinctions. Although a growing body of literature on corridors exists, much of this work is narrow in scope and precludes generalization to larger, community-level situations (Tewksbury et al. 2002).

The term ‘‘corridor’’ has been used in a variety of contexts (see Hess and Fischer 2001; Simberloff et al. 1992); we follow the definition provided by Beier and Noss (1998:1242) of a corridor as, ‘‘a linear habitat, embedded in a dissimilar matrix, that connects two or more larger blocks of habitat and that is proposed for conservation.’’ The traditionally proposed functions of corridors are to increase movement rates between habitat patches, to increase population densities in habitat patches, and to increase gene flow between habitat patches (Beier and Noss 1998). These effects have been posed as effects on populations, and corridors have been evaluated rigorously in recent years with regard to their ability to promote movement (Andreassen et al. 1996; Bowne et al. 1999; Coffman et al. 2001; Collinge 2000; Danielson and Hubbard 2000; Haas 1995; Haddad 1999a; Haddad et al. 2003; Laurance and Laurance 1999; Lorenz and Barrett 1990; Niemela 2001; Tull and Krausman 2001) and to alter demography or genetics among subpopulations (Aars and Ims 1999; Aars et al. 1999; Anderson and Danielson 1997; Andreassen and Ims 2001; Coffman et al. 2001; Fahrig and Merriam 1985; Haddad and Baum 1999; Niemela 2001; Ruefenacht and Knight 1995; Schmiegelow et al. 1997).

The impact of corridors will likely span entire communities (Simberloff and Cox 1987). In the case of corridor effects on predator–prey interactions, the responses of both predators and prey to corridors may differ, potentially affecting population persistence of predators, prey, or both. In microcosm experiments, Burkey (1997) and Holyoak (2000) found connectivity to lead to reduced extinction times for predators and prey. Larger-scale studies have demonstrated that the movements of predators in fragmented landscapes will affect the persistence of

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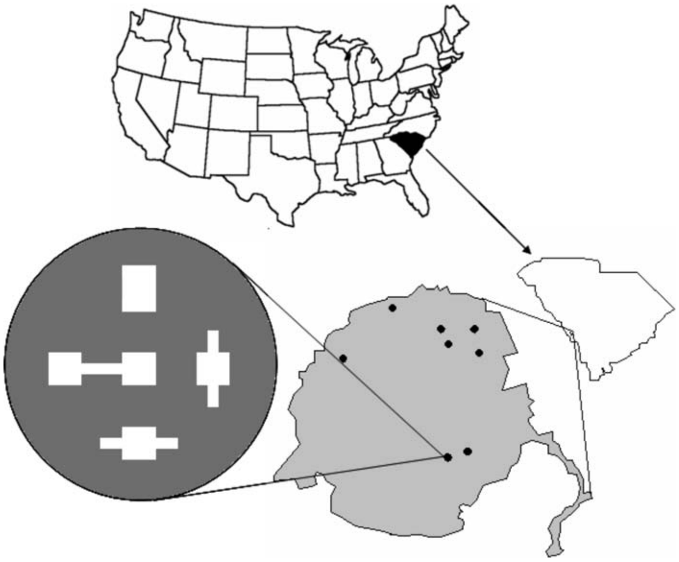

FIG. 1.—Location of the Savannah River Site in South Carolina, and positions of the 8 experimental blocks. Each experimental block is composed of 5 patches.

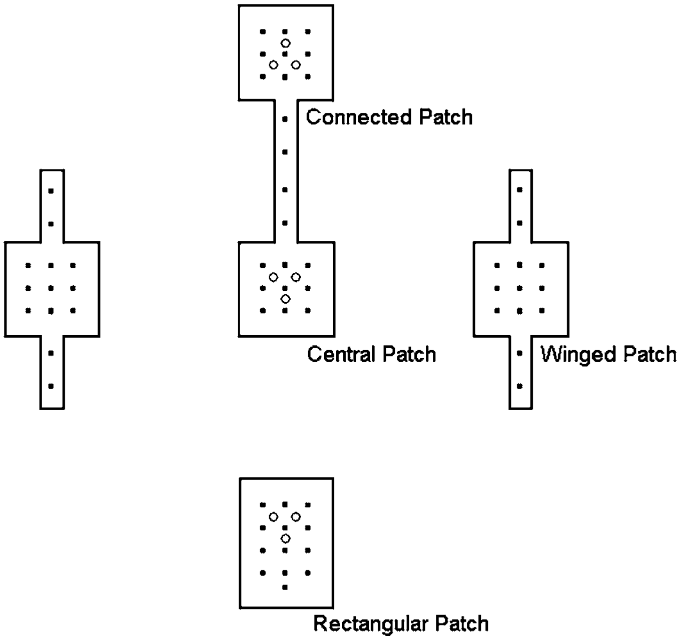

FIG. 2.—Layout of an experimental block. Four peripheral patches surround 1 central patch. The peripheral patches are either connected to the central patch by a linear corridor or are unconnected. Filled squares represent locations of small mammal traps. Open circles represent locations of foraging trays.

prey (Bjornstad et al. 1999) and predators themselves (Namba et al. 1999). Prey have been shown to alter their foraging (e.g., through reduced foraging, increased vigilance, or antipredator behavior such as refuging—Brown 1999; Lima 1998) and movement (Fraser and Cerri 1982; Gilliam and Fraser 2001) behavior when faced with increased predation risk, and the results of these behavioral changes may influence population dynamics in a patchy environment (Sih and Wooster 1994).

Small mammals are known to be affected by corridors (Aars et al. 1999; Andreassen et al. 1996; Coffman et al. 2001; Fahrig and Merriam 1985; Haddad et al. 2003) and are also known to respond to predation risk in their environment (Abramsky et al. 1996; Brown 1992, 1999; Dickman and Doncaster 1984; Epple et al. 1993; Herman and Valone 2000; Kotler 1992; Kotler et al. 1993, 1994). We designed a replicated experiment to explore the responses of small mammals to increased perceived predation risk in a fragmented landscape with corridors. We did this by measuring behavioral changes in mice before and after the addition of predator urine (an olfactory predator cue) to parts of our study system. Specifically, we tested the following hypotheses regarding prey movement, abundance, and foraging behavior in relation to increased perceived predation risk. First, prey will move to connected patches at a higher rate than to unconnected patches upon introduction of an olfactory predator cue. Second, patches connected to those treated with an olfactory predator cue will show higher prey densities than treated patches or unconnected patches. Third, prey will shift their foraging to connected patches with lower perceived predation risk in the presence of a predator cue.

MATERIALS AND METHODS

Study site.—This study was conducted from May through August 2001 at the United States Department of Energy's Savannah River National Environmental Research Park, South Carolina. All sampling was carried out in a network of 40 open-habitat patches created by clear-cutting and burning pine forest between October 1999 and April 2000. These 40 patches are arranged into 8 replicate blocks (Fig. 1). The forest matrix surrounding each block is densely planted loblolly (*Pinus taeda*) and longleaf pine (*P. palustris*) between 40 and 50 years old. This managed forest matrix has a closed canopy with very little understory growth and thus contrasts sharply with the patches.

Each block is made up of a square, 1-ha central patch surrounded by 4 peripheral patches, each 150 m away. One of these peripheral patches is connected to the central patch by a 25-m-wide clear-cut corridor (Fig. 2) and is hereto referred as a "connected" patch. The remaining 3 peripheral patches are not connected to the central patch and are either rectangular or winged in shape (Fig. 2), although these may be simply considered "unconnected patches." The orientation of the corridor relative to the central patch in each block was randomly assigned to control for any directional movement bias.

Study species.—Old-field mice (*Peromyscus polionotus*, Rodentia: Muridae) are the most commonly captured species at our study site (Cothran et al. 1991). This species is restricted to open, ephemeral, grassy habitats such as regenerating clear-cuts (Golley et al. 1965) and is rarely found outside these habitats (B. Danielson, pers. comm.). Juvenile *P. polionotus* usually settle within a few hundred meters (average 160 m) of their natal area (Swilling and Wooten 2002) and occupy home ranges of less than 4,000 m^2 (Swilling and Wooten 2002), although they have been known to disperse several kilometers (Smith 1968). Cotton mice (*P. gossypinus*) also were frequently captured in our study sites. *P. gossypinus* is typically associated with bottomland hardwood and pine forest but also occupies a variety of other habitats (Golley et al. 1965).

Small mammal trapping.—Livetrapping was conducted 4 times during the summer of 2001 following guidelines of the American Society of Mammalogists (http://www.mammalogy.org/committees/index.asp). Sherman live-trap (H. B. Sherman Traps, Inc., Tallahassee, Florida) grids were set at densities of 9 traps/ha in the central patches and 9.45 traps/ha in the peripheral patches (including wings and corridors) for a total of 61 traps per block (Fig. 2). Each trapping session consisted of 2 days of prebaiting (traps left open but not set) followed by 5 consecutive days of trapping. All trapping sessions were separated by 2 weeks, except for a single 1-week period that separated the 2nd and 3rd sessions. Traps were baited with whole oats during trapping sessions and were left open, but not set, during the weeks between trapping sessions. All traps were checked between 0530 and 1100 h during each day of trapping. Every individual captured was marked with a uniquely numbered Monel-1 ear tag (National Band and Tag Co., Newport, Kentucky) and its sex and location were recorded.

Predator treatment.—We conducted predator manipulations by introducing predator urine into one-half of the blocks after the 2nd trapping session and continuing through the end of the study. We used a before–after-control-impact design (Underwood 1994) to control for any temporal effects that might otherwise be attributed to the predator treatment. Under this design, we manipulated only one-half of the blocks and were therefore able to make before–after comparisons in both the control and treated replicates. Small mammals were never captured in the central patches of 2 of the 8 blocks and these had very few individuals in general. Therefore, these blocks were excluded from the predator manipulation and from all behavioral studies.

We applied bobcat urine (Sterling Fur & Tool Co., Sterling, Ohio) to imply the presence of a small mammal predator in the central patches of 3 randomly chosen blocks. We note here that we chose to examine the response of prey to predator cues rather than the effects predators may have on prey in this system under the assumption that the perception of predation risk is not necessarily related to actual rate of predation (Abrams 1993; Lima 1998). We did not necessarily intend to accurately mimic bobcat scent marking patterns but rather to imply, through manipulation of specific patches of our study system, areas of differential predation risk. We chose bobcat urine because bobcats are native to the study site, known to be relatively abundant, and are efficient predators of mice and other small mammals (Cothran et al. 1991). Bobcat urine has been shown to alter the behavior of deer (Swihart et al. 1991) and woodchucks (Swihart 1991).

We applied the urine in a grid of dispensers spaced approximately 6.5 m apart over the entire trapping grid (Fig. 1) for a total of 169 dispensers per treated patch. The dispensers were constructed of plastic film canisters with four 0.5-cm holes punched around the top, below the lid. Each dispenser contained a cotton ball and was filled with 30–35 ml of urine. The dispensers were duct-taped to 6.3-cm nails and driven into the ground. After 1 week, we refilled dispensers with fresh bobcat urine and did not remove the dispensers for the duration of the study.

Foraging activity.—Giving-up densities are measures of foraging activity that quantify the density of resources at which the cost of foraging outweighs the benefits (Kotler 1992). Giving-up densities can be used to measure changes in foraging behavior related to changes in the perception of predation risk (Brown 1999; Kotler 1992; Kotler et al. 1993). To study foraging activity within the blocks, we measured seed removal from covered plastic trays filled with sand and whole millet seed. The foraging trays were constructed of square (11 × 27 × 27-cm) plastic food storage containers, each with two 2.5-cm holes drilled on adjacent sides to allow mice access to the trays. Foraging trays were placed in 3 patches in each block (central, connected, and unconnected-rectangular; Fig. 2). Lids were left on trays to exclude rain and larger (avian and other mammal) seed predators, and the trays were located under cover of shrubs and small trees. The trays were arranged in a triangular configuration 15–18 m apart in the center of each patch (Fig. 2).

We introduced the foraging trays into the patches in late April 2001 and then periodically checked and reset them with millet for 3 weeks before data collection began. During data collection periods, we used a consistent density of 3.16 g ± 0.04 *SE* (542 ± 6.9 seeds) of millet seed in 1 liter of dry sand in all foraging trays. We checked all trays every 3 days for 3 weeks before and after the predator manipulation. If there was evidence of foraging activity (excavation, mouse footprints, and feces) in a tray, we collected the sand and seed mixture and replaced it with fresh sand and millet seeds. Trays that had not been used were left alone. Ants were present in and around some trays but there was no evidence to suggest that they removed any seeds. We then sifted the collected sand from each tray and counted the remaining seeds.

Statistical analysis.—To analyze foraging data, we calculated the average number of seeds left in all foraging trays for each patch in the 6 blocks both before and after manipulation. Values from unused trays were excluded from analysis to normalize the data set. This resulted in 1 value per patch (3 patch types times 6 blocks equals 18 total patches used in this study) from before the manipulation and 1 value per patch after the manipulation. We used a multivariate analysis of variance (MANOVA) to generally assess the effects of predator treatment (treated versus untreated blocks) and time period (before or after treatment) on foraging in the 3 patch types (central, connected, and unconnected). We calculated the relative change in number of seeds remaining in all patch types of treated replicates. We used the before–after-control-impact design to control for any effects of time on foraging activity. To do this, we performed a 1-tailed *t*-test on the difference in seed count values before and after predator manipulation for each patch type of the treated and untreated replicates. Thus, the change in foraging activity in a given patch type is equal to the mean number of seeds remaining after the predator treatment minus the mean number of seeds remaining before treatment. Positive results of this calculation indicate a reduction in foraging activity; more seeds remaining indicates less removal. Because each patch type (central, connected, and unconnected) in each treatment category (treated or untreated) was replicated 3 times, the *t*-tests are based on 3 values. We used 1-tailed *t*-tests because we were testing for the specific result that foraging activity would decrease in central patches and increase in connected patches of treated blocks after predator manipulation.

We tested changes in foraging between pairs of patch types to examine how connectivity influenced foraging in patches adjacent to treated patches. This was done by calculating change in foraging activity between patches (Δ)

$$\Delta = (\mathrm{P} - \mathrm{C})_{\mathrm{after}} - (\mathrm{P} - \mathrm{C})_{\mathrm{before}} \tag{1}$$

where P represents mean number of seeds remaining in a peripheral patch (connected or unconnected), C represents mean number of seeds remaining in a central patch, and "before" and "after" refer to periods before and after predator manipulation. Separate tests were performed for both connected and unconnected peripheral patch types. We performed 1-tailed *t*-tests on differences in Δ values between treated and untreated replicates ($n = 3$) based on the prediction that $\Delta < 0$ for treated replicates and $\Delta = 0$ for control replicates.

We conducted correlation analyses to test for corridor effects on foraging activity in both the presence and absence of a perceived predator. We did this by correlating removal in the central patch with seed removal in connected and unconnected patches. Given the before–after-control-impact design, this resulted in more replicates in the absence of a perceived predator ($n = 9$) than in the presence of a perceived predator ($n = 3$) for each correlation analysis.

RESULTS

Interpatch movement and animal density.—Rates of interpatch movement detected by livetrapping for both *Peromyscus*

TABLE 1.—Differences in abundance of *Peromyscus polionotus* and *P. gossypinus* by patch type (central, rectangular, connected, and winged) and by block. The last 2 rows ("treated") represent differences in abundance of *Peromyscus* by patch type after the introduction of an olfactory predator cue into the central patches of treated replicates (ANOVA = analysis of variance).

	Patch type ANOVA			Block ANOVA		
Species	*F*	*P*	*n*	*F*	*P*	*n*
Peromyscus polionotus	0.30	0.70	6	13.94	<0.001	6
P. gossypinus	0.59	0.63	6	4.74	0.01	6
Peromyscus, treated	1.57	0.27	3	—	—	
Peromyscus, untreated	1.70	0.24	3	—	—	

TABLE 2.—Change in foraging activity of *Peromyscus* by patch type after addition of an olfactory predator cue in treated replicates ($n = 3$) only. Unconnected patches were either winged or rectangular in shape (Fig. 2). Negative values indicate less removal and therefore more seeds remaining. Statistics were generated from *t*-tests including both treated and untreated replicates to control for any effects of time on foraging activity.

Patch type	Seeds remaining before addition of cue ($\bar{X}$)	Seeds remaining after addition of cue ($\bar{X}$)	Change in removal (%)	*P*
Central	101.2	181.65	−79.4	0.042
Connected	134.1	54.05	+59.7	0.094
Unconnected	149.1	124.6	+16.4	0.153

species were very low. Six of 188 *P. polionotus* and 3 of 62 *P. gossypinus* moved between patches. Only 4 of these individuals made interpatch moves originating in a central patch and thus we are not able to assess whether or not corridors influence movement. We found no differences in animal density among patch types and no change in density after predator manipulation. Significant block effects were found for each species individually (Table 1) but when both species of *Peromyscus* were pooled, block effects were no longer significant.

Foraging activity.—Because foraging trays were only placed in unconnected patches that are rectangular in shape, all comparisons of foraging data are between central, connected, and unconnected-rectangular patches (Fig. 2). We normalized the foraging data by square-root transformation (Shapiro–Wilk *W*-test, $P = 0.28$). When all 3 patch types (central, connected, and unconnected) were included in the MANOVA as dependent variables, there was a marginal effect of predator treatment on foraging ($F = 3.72$, $P = 0.069$) and no effect of time period ($F = 0.27$, $P = 0.84$). However, when the unconnected patch was excluded (only central and connected patches analyzed as dependent variables), the predator treatment was found to significantly affect foraging activity ($F = 6.71$, $P = 0.023$) and the effect of time was marginally significant ($F = 0.46$, $P = 0.64$).

Foraging activity decreased after predator manipulation in central patches (Table 2) and the change in foraging activity differed significantly ($t = 2.29$, $P = 0.042$) between treated and untreated replicates. Foraging activity was higher in the connected patches of treated replicates (Table 2) after manipulation, although the difference between control and treated replicates was only marginal ($t = -1.58$, $P = 0.094$). Note that replication was low, and, at this effect level, power analysis reveals that 2 more replicates would be needed to achieve statistical significance at alpha of 0.05. Results from the unconnected patches reveal no difference in foraging activity between the treated and untreated blocks as a result of predator manipulation ($t = -1.17$, $P = 0.153$). Analysis of foraging data with equation 1 was used to test for differences in pairs of patch types as a result of predator manipulation. The combination of reduced foraging in the central patch and increased foraging in the connected patch of the treated blocks differed significantly from the control group ($t = -3.59$, $P = 0.011$). A marginally significant difference also was found between control and treatment blocks when we examined changes in foraging in central and unconnected patch types ($t = -2.11$, $P = 0.052$), although this was likely driven by the drastic change in foraging activity in the central patches of treated replicates.

Foraging activity in the central and connected patches was significantly positively correlated ($r = 0.792$, $P = 0.011$, $n = 9$) in the absence of predator manipulation. No such relationship existed between central and unconnected patch types ($r = 0.263$, $P = 0.495$, $n = 9$). Correlation analyses of treated blocks was not possible because replication was low ($n = 3$). Note that these observations come from 6 replicates and are not necessarily independent, although the same relationship holds when only premanipulation data ($n = 6$) are used.

DISCUSSION

Examination of the foraging data we present indicates that corridors significantly affect the behavior of small mammals. The correlation of seed removal in the central and connected patch, and absence of such a correlation between central and unconnected patches (Fig. 3) demonstrates that corridors somehow synchronize small mammal activity among habitat patches. Others (Aars and Ims 1999; Coffman et al. 2001; Fahrig and Merriam 1985; LaPolla and Barrett 1993; Lorenz and Barrett 1990) have shown that small mammals, including *P. polionotus* (Haddad et al. 2003), are affected by habitat corridors, although, to our knowledge, no one has demonstrated such effects on foraging behavior.

The olfactory predator cue we applied significantly reduced foraging in central patches of treated replicates, supporting findings by other researchers (e.g., Brown 1999; Gilliam and Fraser 2001). The effect of predator cue extended beyond the specific patch that was treated, as is evidenced by the MANOVA and paired-patch analyses. Although we found no impacts of either predator cues or corridors on small mammal density, our results demonstrate that olfactory predator cues induce short-term corridor-dependent changes in behavior.

Although we found very few movements between patches, we have reason to believe that our mark–recapture data do not completely represent the movement behavior of *P. polionotus* or *P. gossypinus*. We captured animals in the corridors of several blocks and Brinkerhoff (2002) found evidence through radiotelemetry to suggest that interpatch moves are more frequent than implied by trapping. In that study, individual *P. polionotus* and *P. gossypinus* were found to make multiple interpatch moves over the period of several hours. We did not detect enough interpatch moves through mark–recapture for analysis but these observations are consistent with our foraging data and lend support to the hypothesis that small mammals use corridors to forage among connected patches.

Our results elucidate important differences between types of movement. At the temporal and spatial scale of this study, corridors may have a stronger effect on short-term (i.e., foraging) than long-term (dispersal) movement behavior. We found corridors to significantly affect the foraging activity, but not abundance, of small mammals. These results echo those of Aars and Ims (1999), who found no corridor effects on dispersal of male root voles through mark–recapture in a large-scale corridor system, but found greater than expected rates of allele movement between connected patches. Aars and Ims (1999) attribute their results to short-term mating excursions facilitated by corridors.

The addition of olfactory predator cues to the landscape affected the behavior of small mammals in ways consistent with corridor-facilitated movement. There is substantial evidence that small mammals will alter their foraging behavior when presented with an increased perceived threat of predation (Herman and Valone 2000; Jacob and Brown 2000; Kats and Dill 1998; Kotler et al. 1993; Rosell 2001) and *P. polionotus* has been shown to switch to safer but lower-quality food items under increased predation risk (Phelan and Baker 1992). However, such changes in behavior are not always predictable and may be counterintuitive (Pusenius and Ostfeld 2000, 2002). As expected, we found reduced foraging in the central patches of the treated replicates as evidenced by a higher mean number of remaining millet seeds in foraging trays. This result can be best explained in one of two ways. One explanation is that the rodents reduced foraging activity and increased refuging behavior. This phenomenon has been demonstrated by other small mammals under increased perceived predation threat (Abramsky et al. 1996; Lima 1998).

Another explanation for this result is that the prey moved, shifting foraging activity to what are perceived to be safer areas (i.e., those without an added predator cue). Evidence for interpatch movement is substantiated by our finding that corridors act to synchronize foraging activity in the absence of a predator cue. Furthermore, we found that corridors and predator treatment do have interactive effects. Foraging activity was marginally higher in connected patches of treated blocks when compared to untreated blocks but did not change in unconnected patches regardless of treatment (Table 2). Results from paired-patch comparisons further demonstrate that corridor connections and treatment have interactive effects. Results demonstrating similar movement patterns to these have been found for small mammals, as well as other organisms (Grostal and Dicke 2000; Kotler et al. 1993; Lima and Dill 1990).

We chose to examine the response of prey to predator cues rather than the direct effects predators may have on prey in this system. The perception of predation risk is not necessarily related to actual rate of predation (Abrams 1993; Lima 1998), so it is unclear what effects actual predators might have in this system. It is clear from the results of this and other studies (Gilliam and Fraser 1988; Grostal and Dicke 2000; Kotler et al. 1994) that the threat of predation can dramatically alter prey behavior. Small mammals have been shown to respond differently to different olfactory cues (JĘdrzejewski et al. 1993) and therefore a different predator scent may have elicited different changes in prey behavior. Bobcats range over areas much larger than our experimental blocks (Cothran et al. 1991) but we have shown that local manipulation of olfactory information significantly affects rodent behavior. Future field studies of the movements of predators in fragmented systems would do a great deal to elucidate the impacts of corridors on predator–prey interactions.

Implications.—We suggest that the behavior of small mammals is affected by both landscape configuration and risk of predation and that these factors can have interactive effects.

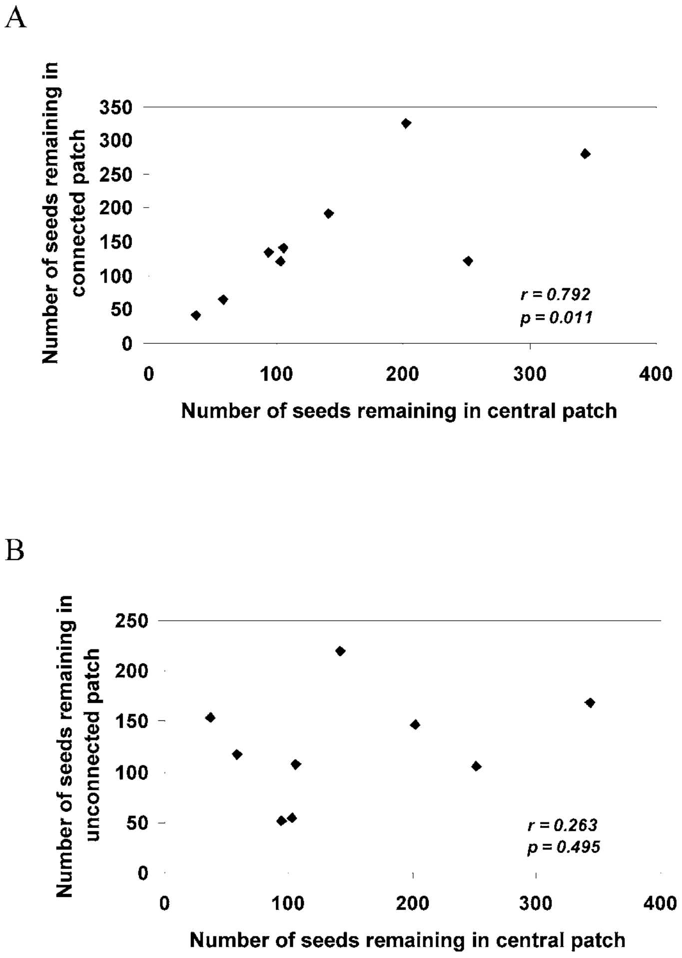

FIG. 3.—Correlation of *Peromyscus* foraging activity in seed removal from foraging trays in 2 pairs of patch types, A) between central and connected patches and B) between central and unconnected patches. Foraging activity was significantly positively correlated between central and connected patches, whereas no such relationship was found between central and unconnected patch types. Symbols indicate mean values. (Patch types are shown in Fig. 2.)

As habitats become increasingly fragmented, it is important to understand how both populations and communities will respond to these changes. Simberloff et al. (1992) suggested that corridors might have detrimental effects on communities by facilitating movements of pathogens (see also Hess 1994) and predators, among other factors. Schoener and Spiller (1996) demonstrate how a novel predator can have a devastating effect on prey, such as might occur upon establishment of a corridor to connect previously separate habitat patches. Organisms may use landscape features such as corridors to locate areas of reduced predation threat or areas of increased resource abundance. We found evidence demonstrating that foraging and movement behavior of small mammals is dependent on habitat connectivity and the presence of olfactory predator cues. These landscape-dependent changes in behavior could have cascading community-level effects. Orrock et al. (2004) found that the impact of different seed predator guilds is influenced by patch shape and connectivity. Thus, it is clear how the presence of corridors might affect seed persistence, seedling establishment, and further plant community dynamics. Such movement would be especially important if habitat patches are associated with differential predation risk that may further alter the behavior of seed predators and herbivores.

Lima and Zollner (1996) stress the need to combine studies of behavior with landscape ecology by expanding the scope and scale of behavioral studies and incorporating more behavioral data into landscape ecology. Recent work has been dedicated to understanding the behaviors of animals in corridor-linked systems, and studies are beginning to link these behaviors to the landscape ecology of these systems (Aars and Ims 1999; Haddad 1999b). Our study does much to contribute to this body of knowledge. We found no evidence to suggest that corridors alter dispersal of small mammals in this system but corridors do affect behavior in other ways, especially when combined with other factors, such as changes in predation risk. To understand how best to manage increasingly fragmented landscapes for the purposes of conservation, it is imperative that we continue to devise experiments and studies to investigate the complex behaviors of species and their interactions in a landscape context.

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