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Corridors have been shown to serve as movement conduits for a wide variety of species, though their effects on interspecific interactions have been largely unstudied. I designed a replicated experiment to investigate corridor-mediated prey responses to predators in a network of open habitat patches surrounded by a matrix of planted pine forest. I used mark-recapture studies and foraging trays to monitor the movements and behaviors of several small mammal species. The presence of predators was artificially manipulated in half of my replicates by applying bobcat urine to specific patches. I then compared the movements of small mammals and changes in foraging activity in the treated and untreated replicates, and tested how corridors affected behaviors and population sizes. I found significant differences in foraging activity between patches treated with predator urine and patches to which they were connected, whereas I found no differences in foraging activity in unconnected patches adjacent to treated patches. Movements detected by mark-recapture were too infrequent for analysis, but were proportionally consistent with previous results showing corridor effects on movement. There were no significant differences in small mammal abundances between connected and unconnected patches. These results suggest that corridors do facilitate movement between habitat patches and prey will preferentially use corridors to forage in patches with reduced predation risk. However, the corridors in this study had no apparent affect on long-term displacement of small mammals.
RESPONSES OF PREY TO THE PRESENCE OF PREDATORS IN A FRAGMENTED LANDSCAPE WITH CORRIDORS

By

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BIOGRAPHY

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INTRODUCTION

Habitat destruction, degradation and fragmentation are of serious conservation concern and have been labeled as the most significant causes of population and species extinction (Hanski 1998). Habitat reduction increases the likelihood of local population extinction due to demographic and catastrophic factors while increased patch isolation reduces the likelihood of recolonization following extinction (Hanski 1997). Wilson and Willis (1975) suggested the use of corridors to mitigate some of the negative effects of habitat fragmentation by allowing continuing immigration to balance out local extinctions. The term “corridor” has been used in a variety of contexts (see Simberloff et al. 1992). I follow the definition provided by Beier and Noss (1998) 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.”

Among the traditionally proposed functions of corridors are: 1) to increase movement rates between habitat patches connected by corridors, 2) to increase population densities in connected compared to unconnected patches, and 3) to increase gene flow between habitat patches (Beier and Noss 1998). Corridors have been evaluated somewhat rigorously with regard to their ability to promote movement (Lorenz and Barrett 1990, Andreassen et al. 1995, Haas 1995, Bowne et al. 1999, Danielson and Hubbard 2000, Laurance and Laurance 1999, Collinge 2000, Coffman et al. 2001, Niemela 2001, Tull and Krausman 2001, Haddad et al. in review) and lead to demographic and/or genetic changes among sub-populations (Fahrig and Merriam 1985, Ruefenacht and Knight 1995, Anderson and Danielson 1997, Schmiegelow et al. 1997, Aars et al. 1999, Aars and Ims 1999, Haddad and Baum 1999, Andreassen and Ims 2001,
Coffman et al. 2001, Niemela 2001). However, in light of this growing body of research, there have been virtually no studies addressing the impacts of corridors on community-level dynamics.

Thus far, most corridor research has focused on single species rather than interactions between species. While single species studies are a logical starting point, clearly the impact of these corridors will span entire communities (Simberloff and Cox 1987). The responses of interacting species are likely to be complex and difficult to sort out. For example, when studying corridor effects on predator-prey interactions, the responses of both predators and prey to corridors need to be considered and the behaviors of each species would impact these interactions. The simplest predator-prey interaction would be one where neither species responds to corridors and each is effectively unable to move between patches. However, differential movement of predators and prey between patches could have drastic effects on population persistence. Prey have been shown to alter their behavior (Brown 1999) and movement (Fraser and Cerri 1982, Gilliam and Fraser 2001) in the light of increased predation risk and the results of this movement may influence population dynamics in a patchy environment (Sih and Wooster 1994). Further, the movements of predators in fragmented landscapes have also been shown to affect predator (Namba et al. 1999) and prey (Bjornstad et al. 1999) population persistence. Given the risk of local population extinction in habitat fragments (Fahrig and Merriam 1985, Hanski 1997, 1998), it is imperative that we better understand the mechanisms that influence population persistence over time.

There are two noteworthy laboratory studies that explicitly address corridor effects on predator-prey interactions. Burkey (1997) and Holyoak (2000) established
microcosm experiments to test the effects of patch connectivity on predator-prey dynamics. Using ciliates, flagellates, and bacteria in a tri-trophic system, Burkey (1997) found not only that fragmented systems reached extinction faster than unfragmented systems, but also that fragmented systems linked by movement corridors reached extinction faster than fragmented systems without corridor connections. In a similar experiment, Holyoak (2000) found that predator persistence in a metapopulation was determined by number of habitat patches, the number of dispersal corridors, and the distance between patches. Both authors suggest several interpretations of their results dealing with the dispersal ability of predators and prey, in neither case is a definitive explanation presented.

There are, to date, no large-scale field studies addressing predator-prey interactions in the presence of corridors. I designed a replicated experiment to study the responses of prey to the presence of predators in a fragmented landscape with corridors. To simplify the experiment, I chose to imply the presence of predators rather than establish predator populations. Auditory (Abramsky et al. 1996), visual (Abramsky et al. 1996) and olfactory (Dickman and Doncaster 1984, Swihart et al. 1991, Eppele et al. 1993, Jedrzejewski et al. 1993, Kats and Dill 1998, Grostal and Dicke 2000, Rosell 2001) predator cues have been shown to significantly affect the behavior of prey organisms. I studied the responses of small mammals to the presence of an implied mammalian predator with the purpose of testing the following hypotheses:

1) If the presence of a corridor affects the movement of prey species, prey individuals will move to connected patches at a higher rate than to unconnected patches upon introduction of an implied predator.
2) If the presence of corridors affects the movement of prey, patches connected
to those with an implied predator will show higher densities of habitat-
restricted prey.

3) If the presence of corridors affects the movement of prey, patches connected
to those with an implied predator would show higher levels of foraging
activity than would patches connected to patches absent of an implied
predator

I tested these hypotheses in an experiment where the area of patches was
controlled but the shape of isolated patches varied. In other words, I tested whether
corridors influenced small mammal populations and behaviors by increasing
connectivity, or by changing other confounded landscape attributes. In addition to my
primary hypotheses I was able to examine the effects of patch shape in addition to
connectivity on the movement behaviors of small mammals.

METHODS AND STUDY SITE

Study site

This study was conducted from May through August in 2000 and 2001 at the U.
S. Department of Energy’s Savannah River National Environmental Research Park,
South Carolina, USA. All sampling was carried out in a network of forty open-habitat
patches created by clear-cutting pine forest. These forty patches are arranged into eight
replicate blocks (Figure 1). Experimental patches were delineated in the late summer of
1999 and the timber harvested between October 1999 and April 2000. After clear-
cutting, all of the patches were burned. The forest matrix surrounding each block is
densely planted loblolly (*Pinus taeda*) and longleaf pine (*P. palustris*), roughly 40 years old. This managed forest matrix has a closed canopy with very little understory growth and thus contrasts sharply with the densely vegetated blocks.

Each block is made up of a square, one-hectare central patch surrounded by four 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 (Figure 2). The remaining three peripheral patches are not connected to the central patch and are either rectangular or winged in shape. The purpose of the rectangular and winged patch shapes is to control for confounding effects that might lead to differences in interpatch movement rates and patch occupancy that could otherwise be attributed to corridors. If corridors act as drift fences, channeling dispersing individuals into connected patches, the winged patches should have densities equivalent to the connected patches. If corridors increase abundance by increasing core habitat area, as suggested by Haddad and Baum (1999), the rectangular and connected patches should have equivalent population densities.

The size of each peripheral patch is equal to the area of the central patch (1 ha) plus the area of the corridor (0.375 ha). To test for within-block variability, half of the blocks have two winged patches and one rectangular patch and the other half have one winged and two rectangular 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

Cotton mice (*Peromyscus gossypinus*, Rodentia:Muridae) and old-field mice (*P. polionotus*) are common small mammal species in the southeastern United States. Cotton mice are typically associated with bottomland hardwood and pine forest but also occupy a variety of other habitats (Golley et al. 1965). Old-field mice are more restricted to open, grassy habitats such as regenerating clear-cuts (Golley et al. 1965). Both species utilize a wide variety of food resources including vegetative and faunal matter (Cothran et al. 1991). These are two of the most abundant small mammal species on the Savannah River Site with cotton mice recorded at 7-10 individuals per hectare and old-field mice at 8-13 individuals per hectare (Cothran et al. 1991).

Small mammal trapping

Live-trapping sessions were conducted four times during each of the two study seasons. Sherman live-trap (H.B. Sherman Traps, Inc., Tallahassee, Florida) grids were set at densities of 9 traps per hectare in the central patches and 9.45 traps per hectare in the peripheral patches for a total of 61 traps per block (Figure 2). Each trapping session consisted of two days of pre-baiting followed by five consecutive days of trapping. All trapping sessions were separated by two weeks, except for a single one-week period that separated the second and third sessions in 2001. Traps were baited with approximately one teaspoon of whole oats and were left open but not set during the weeks between trapping sessions. All traps in all eight blocks were checked between 0530 and 1100 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 patch grid location recorded. Species, body weight, sex, age and reproductive status were also recorded before release. Upon recapture, the individual’s tag number and location were recorded and any changes in reproductive condition were noted.

After the second trapping session of 2001, one of the blocks was dropped from the trapping regime. This area had unusually high densities of fire ant (*Solenopsis invicta*) nests and 100% (n = 2) of the mice captured in this block were killed by fire ants.

*Predator treatment*

I conducted predator manipulations following the second trapping session of the 2001 field season by introducing predator scent into half of the blocks. I used a BACI (before-after-control-impact) design to control for any temporal effects that might otherwise be attributed to the predator treatment. Under this design, I manipulated only half of the blocks and was therefore able to make before-after comparisons in both the control and treated replicates. Small mammals were never captured in the central patches of two of the eight blocks. One of these blocks, described earlier, had exceedingly high densities of fire ants. These two blocks had very few individuals in general and were excluded from the predator manipulation. I applied bobcat urine (Sterling Fur & Tool Co., Sterling, Ohio) to imply the presence of a small mammal predator in the central patches of three randomly chosen blocks. I chose bobcat urine because bobcats are endemic 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 behaviors of deer (Swihart et al. 1991) and woodchucks (Swihart 1991). I applied the urine in a 13 x 13 grid of dispensers spaced roughly 6.5 m apart. The area of the grid of dispensers completely overlapped the trapping grid. The dispensers were constructed of plastic film canisters with four 0.5 cm holes punched around the top, just below the lid. Each dispenser contained a cotton ball and was filled with 30-35 ml of urine. The dispensers were duct-taped to 6.2 cm nails and driven into the ground. After one week, I refilled the dispensers with fresh bobcat urine.

Foraging trays

To measure foraging activity within the blocks, I measured seed predation from covered plastic trays filled with sand and whole millet seed during the 2001 season. The foraging trays were constructed of square (12” x 12” x 4.5”) plastic food storage containers, each with two 1-inch holes drilled on adjacent sides. I arranged three trays in the central patches, connected patches, and unconnected rectangular patches of the six blocks (Figure 2). The two blocks excluded from the predator manipulation were also excluded from the foraging study due to exceedingly low small mammal densities and inactivity in the foraging trays. The lids were left on the trays to keep rain and larger seed predators out, and the trays were located under cover of shrubs and small trees. In blocks where there were two rectangular patches, only one was used in the foraging study. The trays were arranged in a triangular configuration 15-18 m apart in the center of each patch (Figure 2). I introduced the foraging trays into the patches in late-April/early-May 2001 and then periodically checked and reset them with millet for three weeks before data collection began. During data collection periods, I used a consistent
density of $3.16 \pm 0.04$ g ($542 \pm 6.9$ seeds) of millet seed in one liter of dry sand in all of the foraging trays. I checked all trays every three days for the weeks before ($n = 12$) and after ($n = 12$) the predator manipulation. If there was evidence of foraging activity in a tray, I collected the sand/seed mixture and replaced it with fresh sand and 3.16 g of millet. Trays that had not been used were left alone. I then sifted the collected sand from each tray and counted the remaining seeds.

*Radio telemetry*

In an attempt to directly monitor movement behavior, I used radio collars to track the locations of both *Peromyscus* species during the 2000 season. I collected data from nine individuals (5 *P. polionotus* and 4 *P. gossypinus*) in six of the eight blocks. Individuals were captured in Sherman live-traps, were fitted with model 377-C collar transmitters (Advanced Telemetry Systems Inc., Isanti, Minnesota) and were given between 36 and 60 hours to acclimate to the transmitters before data collection began. I located individuals and recorded data at night between dusk and 0300. In addition to time and location of individuals within a block, I recorded microhabitat information of observed small mammal location. I waited no less than one hour between subsequent locations for each individual to minimize autocorrelation of data points (White and Garrott 1990). I also recorded several locations for each individual during daylight hours at intervals of no more than one point per day. Although I followed few individuals ($n = 9$) and could not perform rigorous analysis on these data, anecdotal evidence from this aspect of the study provided insights into *Peromyscus* movement within the blocks.
Analysis

To test for differences in small mammal density among the different patch types (central, rectangular, connected and winged), I used a randomized block ANOVA analysis. I calculated density as number of individuals per hectare. I calculated movement rates based on the trapping data by dividing the number of individuals of each species that were captured in two or more patches by the total number of individuals of that species captured during the study for each block. I compared proportions of individuals moving from a connected patch to rectangular, winged, and connected patches. Since the movement rates were extremely low, analysis on movement data was not possible.

I calculated the average number of seeds left in all foraging trays for each of the three patches in the six blocks both before and after manipulation. For each patch type (i), I performed a one-tailed t-test on the difference (Equation 1) in the values of the treated and untreated replicates before and after predator manipulation.

Equation 1

\[ \text{Change in seed predation}_i = (\text{Mean seeds remaining after}_i - \text{mean seeds remaining before}_i) \]

Since each patch type in each treatment category was replicated three times, the t-tests are based on the average of three numbers. One-tailed analyses are possible in the examination of the responses of each patch individually because I am testing for the specific result that foraging activity would be lower in the central patches and higher in the connected patches of the treated blocks.
Additionally, I used a two-tailed t-test to examine the effects of predator manipulation across patch types. To compare central (A) and connected (B) patches, I calculated the difference in mean number of seeds remaining across patches (Equation 2).

\[
\text{Equation 2}
\]

\[
\text{Change in seed predation} = (\text{mean seeds remaining in patch B} - \text{mean seeds remaining in patch A})_{\text{after}} - (\text{mean seeds remaining in patch B} - \text{mean seeds remaining in patch A})_{\text{before}}
\]

The same calculation was done to look for differences between central and unconnected rectangular patches. These analyses require two-tailed test because a significant result could occur in one of two ways. If a decrease in foraging activity only occurs in the central patches of the treated replicates and not in the connected patches, the response variable calculated by Equation 2 would have been higher in the treated than in the untreated replicates. However, if the increase in foraging activity is limited to the connected patches, the opposite response would have resulted. In both cases, a significant difference implies a response to the predator manipulation though a specific, directional response cannot be predicted. I used an alpha value of 0.05 to test for significance and performed power analyses to determine what levels of replication I would need to achieve significance in all non-significant results given the effect levels I found.
RESULTS

Small mammal trapping

Overall trapping results consisting of number of individuals captured each year, total captures and recapture rates for each species are presented in Table 1. *Peromyscus polionotus* was found in five blocks in 2000 and seven in 2001. *P. gossypinus* was found in seven blocks and 2000 and five in 2001. In all blocks, densities of *P. polionotus* increased and *P. gossypinus* decreased from 2000 to 2001.

I used a randomized-block ANOVA to analyze the difference in density among the different patch types (central, connected, winged and rectangular) for *P. polionotus* and *P. gossypinus*, testing for block and treatment (patch type) effects. I calculated density as number of individuals per hectare. Each individual was counted once; for individuals that were captured in more than one patch, I used the patch type of first capture in this analysis and ignored subsequent recaptures. In 2000, there was no significant difference in abundance among the different patch types for *P. gossypinus* (F = 0.787, p = 0.52) or *P. polionotus* (F = 0.259, p = 0.85) though there were significant block effects (F = 9.961, p < 0.0001 for *P. polionotus*, F = 5.355, p = 0.001 for *P. gossypinus*). Though the relative abundance of each species changed in 2001, there was again no significant difference in density among the patch types for either species (F = 0.48, p = 0.70 for *P. polionotus*, F = 0.59, p = 0.63 for *P. gossypinus*). However, there were again significant block effects (F = 13.939, p < 0.0001 for *P. polionotus*, F = 4.735, p = 0.009 for *P. gossypinus*).

To test for the effects of the predator manipulation on differences in abundance, I used an ANOVA on the number of captures in each patch type before and after the
predator manipulation. For this analysis, I combined the captures of both *Peromyscus* because there was no difference for either species alone and because densities of *P. gossypinus* were too low for independent analysis. The number of individuals captured before the predator manipulation was calculated the same way as in the previous analysis. I used the patch of initial capture after the manipulation to determine post-manipulation densities for any individuals that made inter-patch moves during the period of manipulation. There was no significant difference in the number of individuals captured in each patch type (F = 0.243, p = 0.86) before or after the manipulation in either the untreated (n = 3, F = 1.70, p = 0.24) or treated blocks (n = 3, F = 1.57, p = 0.27).

**Interpatch movement**

The raw movement data for both *Peromyscus* species and for *Sigmodon hispidus* are summarized in Table 2. For *P. polionotus* and for *P. gossypinus*, the mean movement frequency between connected patches is higher than the movement rate between either unconnected patch type (Figure 3). However, there were so few movements that statistical analyses are not reliable.

The telemetry data are not robust enough for analysis but provide interesting anecdotal evidence. Data were gathered from a total of nine mice, four *P. gossypinus* (two male, two female) and five *P. polionotus* (three male, two female). *P. polionotus* were never found outside the boundaries of a patch or corridor (61 observations), whereas *P. gossypinus* were found in the forest matrix 42% of the time (21 out of 50) observations. *P. gossypinus* was not found to move between patches during telemetry while one *P. polionotus* moved twice between patches connected by a corridor.
Foraging trays

I normalized all of the foraging data by square-root transformation (Shapiro-Wilk $W$-test, $p = 0.28$). The change in seed predation before and after predator manipulation, as calculated by Equation 1, showed a significant ($t = 2.29, p = 0.042$) response to the treatment in the central patch as more seeds were left in the central patches of the treated blocks than in the untreated blocks following predator manipulation. This demonstrates reduced foraging activity in the central patches of the treated blocks following the predator manipulation (Figure 4). Foraging activity was marginally higher ($t = -1.58, p = 0.094$) after the manipulation in the connected patches of the treated blocks than in the connected patches of the untreated blocks (Figure 4). At this effect level, power analysis reveals that two more replicates would be needed to achieve statistical significance at alpha of 0.05. Results from the unconnected, rectangular patches show no significant change in foraging activity between the treated and untreated blocks after the predator manipulation ($t = -1.17, p = 0.153$). At this effect level, eight more replicates would be needed to gain significance.

Analysis of the interaction between the central and connected patches shows a significant difference between the treated and untreated blocks following the predator manipulation ($t = -3.59, p = 0.023$). 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. There was no significant difference in the interaction of foraging in the central and unconnected patch types ($t = -2.11, p = 0.100$).
I also approached this data set in another way by ignoring the number of seeds left in each tray and simply count foraging activity as a binary response; either a tray was used on a given night or it was not used. I tallied the number of “hits”, or foraging trays used, before and after the predator treatment for each patch and analyzed these numbers in the same way as the previous data set. This analysis did not produce significant results, likely because there was very little variance in the number of hits per patch. In an attempt to combine these measurements, I derived a third analysis. As in the first analysis, I used the number of seeds left in each tray as the measure of foraging activity. However, in this analysis, the counts of the remaining seeds were used, just as in the first analysis, and the missing “non-hit” values were replaced with 542, the average number of seeds in 3.16 grams of millet. In this analysis, each patch mean was derived from twelve data points where 542 was substituted for the missing data. The response variables were calculated the same way as in the previous analyses (Equations 1 and 2). The results, while similar in proportion to those generated from the first analysis, were not significant and the data were not normally distributed upon square-root transformation (Shapiro-Wilk $W$-test, $p = 0.014$).
DISCUSSION

This study is among the first to focus on predator-prey interactions in the presence of corridors in a large-scale patchy landscape. My results demonstrate that corridors affect small mammal movement behavior and that there is a significant corridor effect on the foraging behavior of small mammals in the presence of a perceived predator. Furthermore, *Peromyscus gossypinus* and *P. polionotus* appear to move at greater frequency between patches connected by corridors than between unconnected patches, though these results are not statistically significant due to low total movement frequency. While other studies (Danielson and Hubbard 2000, Andreassen and Ims 2001) argue that corridors do not influence the likelihood of dispersal from a patch for small mammals, my results show that corridors affect small mammal movements. Several studies in recent years have demonstrated that large-scale corridors are useful in increasing movement rates for certain species but virtually none have examined the effects of corridors on community dynamics.

*Effects of connectivity and predation risk on foraging behavior*

I found a significant corridor effect on foraging behavior in response to the predator treatment. As expected, there was a decrease in foraging activity in the central patches of the treated replicates, as evidenced by a higher mean number of remaining millet seed in the foraging trays. There is substantial evidence showing that small mammals will alter their foraging behaviors when presented with an increased perceived threat of predation (Kotler et al. 1993, Kats and Dill 1998, Herman and Valone 2000, Jacob and Brown 2000, 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, my results demonstrate a combined effect on behavior of increased predation risk and the presence of corridors linking habitat patches. I found a marginal increase in foraging behavior in the connected patches of the treated replicates and no difference in the unconnected patches between treated and untreated replicates. In other words, the predator treatment only affected individuals in the corridor-linked patches. The significant decrease in foraging activity in the central patches of the treated replicates was accompanied by a corresponding increase in foraging activity in the connected patches of these replicates. No such interaction was found between the source patch and unconnected patch of the treated replicates. These results imply that there is movement between connected patches under an increased perceived risk of predation.

**Corridor effects on interpatch movement**

There is ample evidence to suggest that some small mammals move at greater frequency between patches connected by corridors than between unconnected patches (Fahrig and Merriam 1985, Lorenz and Barrett 1990, LaPolla and Barrett 1993, Coffman et al. 2001, Haddad et al. *in review*). I was not able to provide statistically significant evidence to support these previous studies, but I did find similar trends in movement between patches. The mark-recapture data showed very few individuals to move between patches. Of those that did move, there was at least double the frequency of movement between connected than unconnected patches (Figure 3).

The difference in interpatch movement frequency between this and previous studies might be explained by a number of factors. Most of the corridor research that has
been done has been uncontrolled and unreplicated. Two studies that have been conducted in a replicated, experimental landscape (Bowne et al. 1999, Danielson and Hubbard 2000) have used transplanted rather than naturally occurring individuals. It is reasonable to assume that resident individuals would behave differently than introduced individuals (Bowne et al. 1999). In particular, the released animals made more inter-patch movements than the feral animals in my study. While the movement data from my study are too few to lend themselves to detailed analysis, they are based on feral animals in a replicated landscape, and the rates of movement between connected patches are suggestive of a corridor effect. I found that *Peromyscus polionotus* and *P. gossypinus* are at least twice as likely to move to a patch connected by a corridor than to a patch not connected by a corridor (Figure 3). While the frequency of movement for either species is too low for analysis (Table 2), the results for *P. polionotus* are similar to those found by Haddad et al. (*in review*).

I was further able to gain anecdotal evidence to support a corridor effect from my radio telemetry data. Two interpatch moves were made during periods of telemetry and both were between connected patches. An individual *P. polionotus* moved from the central patch to the connected patch and back to the central patch of an block over the period of several hours in one night. This demonstrates that it is possible for an individual to make multiple inter-patch moves in one night, as may be characteristic of short-term foraging. Furthermore, *P. polionotus* was never found outside patch or corridor boundaries suggesting strong habitat preference. *P. gossypinus*, on the other hand, was frequently found in the forest matrix and was never observed to make an inter-patch move during periods of telemetry.
Of the *Peromyscus* species, *P. polionotus* was more likely than *P. gossypinus* to move between connected patches based on the overall movement data. Both species, however, moved more frequently from a connected patch to another connected patch than to either unconnected patch type (Figure 3). Of the 8 interpatch moves originating in a connected patch made by *P. polionotus*, 5 (63%) were between connected patches while 4 of the 8 (50%) inter-patch moves made by *P. gossypinus* were between patches linked by a corridor (Table 2).

It seems clear from this and other studies that certain species are more likely to use corridors than others. Fahrig and Paloheimo (1988) demonstrated that characteristics such as dispersal distance of a species can significantly alter the effects of habitat fragmentation. Haddad (1999) found that habitat specialist butterflies are more likely to use corridors in travelling between patches than habitat generalist butterflies that are more capable of travelling through matrix habitat. Similarly, I found that *P. polionotus*, an open habitat specialist, is more likely to move between clear-cut patches using corridors than *P. gossypinus*, a habitat generalist. *Sigmodon hispidus*, though typically described as an open-habitat specialist (Lidicker et al., 1992), was not influenced by the presence of corridors in moving between patches. A survey of ten forest stands on the Savannah River Site consisting of a total of 1500 trap-nights found only one *S. hispidus* and no *P. polionotus* (Danielson and Hubbard 2000), while *P. gossypinus* are much more abundant in this habitat.

*Differences in abundance among different patch types*
I found no significant differences in *Peromyscus* abundance among the four patch types in any analyses. However, this non-significance has important ramifications. The design of the blocks was specifically established to tease out differences in density based on patch shape. I found no evidence that corridors serve as drift fences or that they allow for greater density by increasing core habitat area. Both *P. polionotus* and *P. gossypinus* seemed to be evenly distributed across the available habitat patches in both years of this study (Figure 5). Habitat area was the only predictor of small mammal abundance; there was no influence of patch shape, connectivity or relative proportion of edge habitat. In contrast to Haddad and Baum’s (1999) findings with butterflies, I found no effects of corridors on small mammal density. My results are in agreement with those of Danielson and Hubbard (2000), who argued against a drift-fence effect, instead finding equal abundances of *Peromyscus polionotus* in both connected and unconnected patch types.

I found no evidence to suggest that the predator manipulation had any effect on abundance or probability of capture in the treated replicates. Before the treatment there were no differences in *Peromyscus* abundance among the different patch types. As in previous analyses, I combined the capture data for *P. polionotus* with that for *P. gossypinus*. Each species was evenly distributed among the patch types before the manipulation but both species were not present in all blocks. *P. gossypinus* was only captured in all patches of two blocks and *P. polionotus* was only captured in all patches of four blocks. After the manipulation, there was still no significant difference in abundance. Note that with only three replicates of treated and untreated blocks, such a trend would have to be very strong in order to become apparent. Furthermore, the number of captures declined rapidly with each week of trapping. Total captures in weeks
1-4 were 333, 264, 131 and 91. Any trend that may have existed in differences in abundance among the patch types would have been hidden by low capture rates. Similar decreasing temporal trends in capture rate has been found in other studies (Joule and Jameson 1972), though it is not clear what causes this phenomenon.

**Synthesis**

The data from this study support findings of other studies showing that the presence of corridors in a fragmented landscape effects interpatch movement behavior of small mammals. Furthermore, this study demonstrates an important distinction between different types of movement. At the scale of my study, corridors may have a stronger effect on short-term (i.e. foraging) than long-term (dispersal) movement behavior. Aars and Ims (1999) found no corridor effects on dispersal of male root voles through mark-recapture in a large-scale corridor system. Genetic analysis, however, demonstrated that there was a greater than expected rate of allele movement between connected patches. The authors attribute this result to short-term mating excursions facilitated by corridors. The movement data based on trapping and radio telemetry lend support to corridor effects found in previous studies. When combined with the foraging data, a clear and strong argument for corridor effects on small mammal movement emerges. My results suggest that short-term “foraging excursions” occur more frequently between connected than unconnected patches. The small mammals in this study not only moved more frequently between patches connected by corridors but they did so at significantly higher rates in the presence of an implied predator. Another predator-prey movement study demonstrated
the stream fish will dramatically alter their foraging patterns by avoiding areas of increased predation threat (Gilliam and Fraser 1988).

Based on the overall movement rates and telemetry data, *P. polionotus*, a habitat specialist, seems more likely to respond to corridors than *P. gossypinus*, a habitat generalist. It appears that *P. polionotus* move between patches to forage in areas of lower predation risk, and they tend to make these moves between connected patches. The holes drilled in the foraging trays were small enough to exclude *S. hispidus* but did not exclude either *Peromyscus* species. Thus it is impossible to know which species was foraging in each tray. However, given the relative abundance of *P. polionotus* in these patches in 2001 (Table 1), it is reasonable to assume that this species was responsible for the majority of the foraging activity recorded. I speculate that part of the increase in foraging activity in the rectangular patches of the treated blocks may be attributed to *P. gossypinus*. Although *P. polionotus* may have moved between unconnected patches, it is more parsimonious to attribute these results to *P. gossypinus*.

Recapture data are not entirely reliable estimates of small mammal movement. In light of the telemetry and foraging data, it appears that the trapping data to under-represent inter-patch movement. The data suggest that there is some behavioral response to trapping leading to a decrease in trapping success with time. However, small mammal foraging activity, as quantified by the foraging tray data, was consistent with time. Thus a reduction in abundance does not necessarily account for the reduced capture success. The small mammal abundance in any one block was not enough to generate meaningful population parameter estimates. However, such determinants of trap response or
differential likelihood of capture among individuals in the sample population would be quite useful in understanding the decrease in capture success with time.

**Implications**

In light of the growing body of population-level corridor research, the next logical step is to understand how corridors affect interspecific interactions. Among the goals of this study was to determine the response of prey to the presence of predators in a patchy landscape with corridor connections. Simberloff et al. (1992) suggested that corridors might have detrimental effects on communities by facilitating movements of pathogens 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. Burkey (1997) and Holyoak (2000) demonstrate that connectivity is important in predator-prey interactions in microcosm experiments. This study demonstrates that prey, in response to the presence of a non-mobile (implied) predator, will use corridors to move to patches with reduced predation risk. While the link between a real-world field experiment and a controlled laboratory experiment is tenuous, the contrasts between this study and those of Burkey (1997) and Holyoak (2000) are noteworthy. The prey in each microcosm experiment were far less mobile than the predators and thus the predators were able to drive the populations in each patch to extinction before recolonization could occur. With no prey resources, the predators subsequently crashed. With more mobile prey, such an extinction event is less likely. As demonstrated by the small mammals of this study,
mobile prey will readily move between connected patches in the face of an increased risk of predation.

A caveat of this study is that the predators were only implied and thus could not move or have act to reduce the prey population size, but the results are nonetheless intriguing. 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 my system. However, it is clear from the results of this and other studies (Gilliam and Fraser 1988, Kotler et al. 1994, Grostal and Dicke 1999) that the threat of predation can dramatically alter prey behavior. Further field studies of the movements of predators in such a landscape would do a great deal to shed light on these issues and are necessary to truly understand how corridors affect predator-prey interactions. Additionally, long-term studies of predator-prey interactions in the presence of corridors would elucidate demographic trends. It would be imprudent to speculate about future population trends of *Peromyscus* based on these results. However, movement parameters generated by this and other such studies could be used to create models to simulate predator and prey population persistence over time.

Continuation of such multi-species studies in large-scale corridor systems will be of tremendous importance in determining the fate of corridors in future conservation decisions. However, before these decisions are made, it is important to understand what long-term effects corridors would have on dynamic interspecific interactions. Predator-prey relationships, as noted above, may be highly dependent on landscape configuration. The way an animal perceives and responds to a landscape will have cascading effects on other organisms in a given community. Much 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. Lima and
Zollner (1996) stress the need to combine studies of behavior to landscape ecology by
expanding the scope and scale of behavioral studies and incorporating more behavioral
data into landscape ecology. In the context of this experiment, multiple aspects of
behavioral ecology need to be considered before a decision is made regarding the
effectiveness of corridors in conservation. While I found no evidence to suggest that
corridors alter the demographics of small mammals populations in this system, I have
presented evidence that corridors are useful as movement conduits. Movement must be
considered as more than dispersal behavior; clearly short-term movements are facilitated
by corridors and these movements may prove to have drastic effects on this system.
Changes in patch-specific foraging behavior could have effects on other species. For
example, corridor effects on small mammal movement could increase the intensity of
seed predation in connected patches, thus altering community dynamics. In order to
understand how to best 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.

REFERENCES

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Aars, J. and R.A. Ims. 1999. The effect of habitat corridors on rates of transfer and

Abrams, P.A. 1993. Why predation rate should not be proportional to predator density.
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Table 1. Species captured and recapture rates in 2000 and 2001.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number caught</th>
<th>Total captures</th>
<th>Recapture rate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Year</td>
<td>2000 2001</td>
<td>2000 2001</td>
</tr>
<tr>
<td>Peromyscus gossypinus</td>
<td>115 62</td>
<td>458 203</td>
<td>74% (85/115) 74% (46/62)</td>
</tr>
<tr>
<td>Peromyscus polionotus</td>
<td>47 188</td>
<td>174 493</td>
<td>77% (36/47) 61% (114/188)</td>
</tr>
<tr>
<td>Reithrodontomys humulus</td>
<td>6 3</td>
<td>9 9</td>
<td>33% (2/6) 67% (2/3)</td>
</tr>
<tr>
<td>Sigmodon hispidus</td>
<td>8 32</td>
<td>14 102</td>
<td>38% (3/8) 59% (19/32)</td>
</tr>
<tr>
<td>Sylvilagus floridanus</td>
<td>0 3*</td>
<td>0 7</td>
<td>0% (0/0) -</td>
</tr>
</tbody>
</table>

*Two S. floridanus were not tagged. This number represents the number of tagged animals or minimum number known alive.
Table 2. Rates of interpatch movements originating in a connected patch.

<table>
<thead>
<tr>
<th>Species</th>
<th>Individuals making inter-patch moves</th>
<th>Number of inter-patch moves</th>
<th>Number of inter-patch moves to a connected patch</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Peromyscus gossypinus</em></td>
<td>6/177 (3.4%)</td>
<td>8</td>
<td>4/8 (50.0%)</td>
</tr>
<tr>
<td><em>Peromyscus polionotus</em></td>
<td>5/235 (2.1%)</td>
<td>8</td>
<td>5/8 (62.5%)</td>
</tr>
<tr>
<td><em>Sigmodon hispidus</em></td>
<td>2/40 (5.0%)</td>
<td>3</td>
<td>0/3 (0.0%)</td>
</tr>
</tbody>
</table>
Figure 1. Location of the SRS and positions of the eight experimental blocks.
Figure 2. Layout of an experimental unit. Four of the replicates are of this design while the other four have two rectangular patches and one winged patch. Filled squares represent locations of small mammal traps. Open circles represent locations of foraging trays.
Figure 3. Mean (± 1 SE) proportions of individuals moving to either a connected, rectangular or winged patch from a connected patch for *P. gossypinus* and *P. polionotus*. 
Figure 4. Change in mean number of seeds remaining in foraging trays before and after predator manipulation in treated and untreated replicates for each patch type. Raw data failed normality tests; analyses were performed on square-root transformed data.
Figure 5. Number of individuals by patch type for 2000 and 2001. Each dot represents the count from one experimental unit.