PATCH SHAPE, CONNECTIVITY, AND FORAGING BY OLDIELD MICE (PEROMYSCUS POLIONOTUS)

JOHN L. ORROCK* AND BRENT J. DANIELSON

Ecology and Evolutionary Biology Interdepartmental Graduate Program, 353 Bessey Hall, Iowa State University, Ames, IA 50011-1020, USA (JLO)
Department of Ecology, Evolution, and Organismal Biology, 353 Bessey Hall, Iowa State University, Ames, IA 50011-1020, USA (BJD)
Present address of JLO: National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, CA 39101, USA

We examined how corridors and patch shape affect foraging by the oldfield mouse (Peromyscus polionotus) by deploying foraging trays and live traps in experimental landscapes with 3 different patch types: patches connected with a corridor, unconnected patches with projecting corridorlike portions (“winged” patches), and unconnected rectangular patches. Corridors did not lead to different levels of activity of P. polionotus among the 3 patch types. Rather, corridors influenced activity by changing patch shape: foraging in seed trays and total number of captures of P. polionotus tended to be greater at the patch center than at the patch edge, but only in connected and winged patches where corridors or wings increased the amount of patch edge relative to the amount of core habitat in the patch. P. polionotus avoided open microhabitats near the patch edge in winged and connected patches, but not open microhabitats near the patch interior, suggesting that predation risk caused shifts in foraging near edges in connected and winged patches. Foraging in corridors and wings was generally low, suggesting that both are high-risk habitats where predation risk is not ameliorated by proximity to vegetative cover. By changing patch shape, corridors caused changes in within-patch activity of P. polionotus, changing foraging patterns and potentially altering the dynamics of P. polionotus and the seeds they consume.

Key words: corridor, edge, foraging, giving-up density, Peromyscus polionotus, Savannah River Site

Corridors are narrow strips of habitat that connect disjunct patches of habitat (e.g., Beier and Noss 1998; Haddad et al. 2003; Mabry and Barrett 2003; Rosenberg et al. 1997). By promoting among-patch processes such as movement, gene flow, and recolonization, corridors may have beneficial conservation value (Andreassen et al. 1996; Coffman et al. 2001; Haddad et al. 2003; LaPolla and Barrett 1993; Mech and Hallett 2001; Tewksbury et al. 2002). However, understanding the full impact of corridors as conservation tools requires an understanding of how corridors may affect within-patch processes, if only because patch geometry can affect habitat quality and individual behavior (Fagan et al. 1999; Ries et al. 2004). For example, corridors influence patch shape because corridors are generally long, linear elements with a large amount of edge relative to the patches they connect (Haddad and Baum 1999; Rosenberg et al. 1997). For edge-avoiding organisms, a patch with a corridor may have less usable habitat compared to a patch of the same size that is more rounded in profile. In this case, a better conservation strategy might be to increase size of the habitat patches, rather than invest limited resources in connecting the patches with a corridor.

We examined the effect of patch shape and connectivity on activity of the oldfield mouse (Peromyscus polionotus). Oldfield mice are common habitat specialists in early successional habitats in the southeastern United States (Davenport 1964). Previous work on P. polionotus has focused primarily on how corridors affect movement and dispersal (Danielson and Hubbard 2000; Haddad et al. 2003; Mabry and Barrett 2003), abundance (Mabry et al. 2003), and home range (Mabry et al. 2003). Mabry et al. (2003) found that P. polionotus was captured more frequently in the interior of patches, suggesting that P. polionotus does respond to patch edges and corridors. However, corridor length varied among connected patches, and patch shape was not manipulated independently of connectivity (Mabry et al. 2003). We focus on how both corridors and patch shape affect activity of P. polionotus, and we specifically address a potential mechanism that could produce shifts in foraging behavior: spatial shifts in predation risk.

* Correspondent: orrock@nceas.ucsb.edu

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Examining the effect of corridors on activity requires manipulation of connectivity and patch shape by using 3 patch types: a connected patch that is connected to another patch via a corridor; a patch that is unconnected but still has edgy, corridorlike extensions; and a patch with the same area as the other patches, but without linear extensions (Fig. 1). Use of these 3 patch types allows discrimination among responses due to connectivity, responses due to edge, and responses due to both. For logistical reasons, large-scale studies that meet these criteria are virtually nonexistent (see reviews in Beier and Noss [1998] and Rosenberg et al. [1997]). We used an experimental landscape with patches of similar size that varied in shape and connectivity to examine whether corridors influence foraging of *P. polionotus* by affecting patch connectivity, patch shape, or both patch connectivity and patch shape. Specifically, we examined how patch shape and connectivity may lead to differences in foraging within and among patches, and whether foraging patterns suggest that predation risk is the mechanism responsible for shifting foraging patterns.

**Materials and Methods**

Experimental landscape.—The experiment was conducted in 2 replicated blocks (the “experimental units” in Orrock et al. [2003]) created at the Savannah River Site, a National Environmental Research Park near Aiken, South Carolina. Each block consisted of 5 open patches created during the fall and winter of 1999 by clear-cutting mature pine forest followed by prescribed burning (Fig. 1). In each block, there were 3 different patch types: connected, rectangular, and winged (Fig. 1). Connected patches were 1-ha patches joined by a 25-m-wide corridor that was 150 m in length; one-half of the corridor is considered to be in each connected patch (Fig. 1). Rectangular patches consisted of a 1-ha square patch with 0.375 ha of additional area, representing the area added by the corridor (Fig. 1). Winged patches consisted of a 1-ha square patch with 2 extending “drift-fence” sections, each 75 m long and 25 m wide (Fig. 1). Two connected patches and 2 rectangular patches were in each block, yielding a total of 4 connected patches, 4 rectangular patches, and 2 winged patches. Although 6 other blocks existed (Orrock et al. 2003), they were not used because *P. polionotus* was rarely captured there during ancillary trapping sessions.

**Predictions that differentiate the effects of patch shape and connectivity**.—Our design allowed us to determine the relative importance of connectivity and shape because each makes a unique prediction regarding among- and within-patch effects. Although patches were of similar area (connected patches were 1.19 ha and winged and rectangular patches were each 1.38 ha), patch types differed in their connectivity and in the relative amounts of edge and area habitat. This is illustrated by the area to perimeter ratio for each patch type: 22.62 for connected patches, 19.64 for winged patches, and 28.95 for rectangular patches. The small difference in total area between connected and unconnected patches does not change the qualitative order of our predictions. Rather, if foraging is greatest in connected patches, despite the slightly reduced overall area of connected patches, we have a more conservative test for corridor effects.

We examined foraging at different locations within a patch (Fig. 1), to determine the role of patch shape and connectivity in affecting within-patch foraging. For example, although patch area is relatively constant, the greater amount of edge relative to core habitat in connected and winged patches may cause *P. polionotus* to disproportionately allocate foraging activity near the center of these patch types. Using the terminology from Fig. 1, this assumption predicts that foraging in core locations in connected and winged patches will be equal, and both will receive greater foraging than the core of rectangular patches (i.e., connected core = winged core > rectangular core). Conversely, the reduced amount of edge relative to core habitat in rectangular patches may lead to more equitable foraging over the entire patch by *P. polionotus* (i.e., rectangle core = rectangle edge). As such, if the within-patch behavior of *P. polionotus* is influenced by edge, we expect that the difference between foraging at the edge and at the core would be greatest in connected and winged patches, and least in rectangular patches. Where predation risk is the mechanism producing differences in foraging among locations, we expect differences in foraging between paired foraging trays where 1 tray is protected from predators and 1 tray is exposed to predators (see below).

Corridors and patch shape also may change among-patch foraging of *P. polionotus*. If corridors affect rodent foraging by affecting connectivity alone, foraging should differ between connected and unconnected patches (connected patches ≠ winged and rectangular patches). If corridors affect rodent foraging by changing patch shape, foraging should be similar between connected and unconnected patches of the same shape (winged patches = connected patches;
winged and connected patches \(\neq\) rectangular patches). If patch shape and connectivity are important, foraging should differ between connected and unconnected patches, as well as between unconnected patches of different shape (all 3 patch types differ).

**Rodent foraging.**—We used paired foraging trays placed at different locations within each patch type (Fig. 1). Within each pair of trays, 1 tray was placed below vegetative cover (the “sheltered” tray), and the corresponding tray (the “exposed” tray) was placed outside of cover, \(<1\) m away. Pairs of trays were placed in the center of each patch (core location) and 12.5 m from the edge of each patch (edge location). Within each connected patch, a pair of trays also was placed 12.5 m from the edge within the corridor (corridor location). Similarly, a pair of trays also was placed 12.5 m from the edge within 1 randomly selected wing of each winged patch (wing location; Fig. 1).

Each tray was a \(27 \times 27 \times 11\)-cm plastic storage container filled with 1 liter of sand. Holes 2.5 cm in diameter were drilled in 2 sides to allow mice to enter and exit the tray. Each tray contained a constant volume of millet seeds (3.7 ml) thoroughly mixed into the sand, and was covered with a plastic lid to exclude rain and avian granivores. As a foraging rodent depletes the seeds within a tray, diminishing returns are realized (Brown 1988; Morris and Davidson 2000). Eventually, the benefits of continued foraging are outweighed by the costs (Brown 1988). This threshold, called the giving-up density (Brown 1988) represents a quantitative measure of the costs of foraging (i.e., metabolic costs, missed-opportunity costs, and predation risk), because a rodent should stop foraging, or “give up” when the cost of foraging equals the (diminishing) rate of gain from foraging. By pairing the trays, it is assumed that missed opportunities and metabolic costs are the same within a pair. As such, the difference between sheltered and exposed trays can be used to quantify predation risk experienced by rodents (e.g., Abramsky et al. 2002; Morris and Davidson 2000), including *P. polionotus* (Orrock et al. 2004).

Trays were established on 6 May 2003 and were left for 3 days at each location before data collection to allow rodents to become accustomed to the tray (Morris and Davidson 2000). From 9 to 13 May 2003, we visited traysdaily. If signs of foraging were noted (hulls, rodent tracks, or fecal pellets), we sieved the seeds from the sand, refilled the tray with a constant volume of millet seeds, and thoroughly mixed the seeds into the sand. On the final day of sampling, all trays were sieved and seeds were collected. This sampling duration allowed us to reduce the confounding effects of additional factors that change predation risk over time (e.g., changes in moon phase—Orrock et al. 2004).

**Rodent abundance and activity.**—We sampled rodents to ensure that *P. polionotus* was the predominant forager in our patches, to obtain a relative estimate of the number of rodents at a location, and to provide a separate metric of rodent activity (i.e., total captures of *P. polionotus*) for comparison with our findings from foraging trays. Four Sherman live traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) were placed at each location from 13 to 17 May 2003. Traps were baited with rolled oats and locked open for the first 2 days. Subsequently, traps were activated and checked daily for the next 3 days (which we had previously found was sufficient to capture \(>75\%\) of unmarked individuals). Captured rodents were identified to species, marked with a uniquely numbered ear tag (National Band and Tag Company, Newport, Kentucky), and released at the site of capture. All field procedures followed established guidelines (Animal Care and Use Committee 1998).

**Data analysis.**—To examine the effect of patch shape and location on overall seed removal, we compared seed removal at each location by using a mixed-model analysis of variance (Littell et al. 1996). The structure of our design represents a blocked, nested split plot, with groups of 5 patches representing blocks (Fig. 1), patch type (connected, rectangular, or winged) representing the main plot, and location nested within patch type representing the split plot. Our analysis accommodates repeated measures taken over time (i.e., we visited the same sites on consecutive days) by using a type 1 autoregressive covariance structure (Littell et al. 1996). Because we were not interested in testing hypotheses regarding time or experimental unit, our statistical model specified day and experimental unit as random effects. Patch type was a fixed main-plot effect and location was a fixed effect nested within patch type. Our comparisons of patch-type effects were not compromised by the nested nature of our design (e.g., corridor locations were only found in connected patches) because analogous results were obtained if patch-type effects were compared by using only observations from core and edge locations (i.e., locations shared by all patch types). Tray microhabitat (sheltered or exposed) was a fixed effect fully crossed with location and patch type. Because we were specifically interested in determining whether *P. polionotus* perceived some locations as safe and some as risky, we dissected the interaction between location and microhabitat into 8 linear contrasts. If rodent activity was never observed at either tray within a pair, that pair was not included in the analysis. Although this resulted in an unbalanced design, it makes our conclusions more robust because we can assume that foraging is not confounded with the presence of mice (i.e., mice must be present for a foraging choice to occur). We also did not include data from 1 location where a cotton mouse (*Peromyscus gossypinus*) was the only rodent captured.

We used a mixed-model analysis of variance to examine trapping data, treating experimental unit as a random effect and patch type and location as fixed effects. Capture data were pooled across the sampling session. Dependent variables examined were the total number of captures at a site (as a metric of total rodent activity), and the total number of unique individuals captured at a location (*M* \(_t\), the number of marked individuals—Slade and Blair 2000). We used *M* \(_t\) because it performs as well or better than closed-population estimation techniques (e.g., the Lincoln–Petersen estimator) when sample sizes are low or animals are not captured at all locations (Slade and Blair 2000).

Before analysis, weights of seeds remaining in each tray were cube-root transformed to improve normality and stabilize variance, as evaluated by using residual plots (Zar 1996). The mean weight of seeds from unforaged trays on the last day of the foraging experiment (2.82 g \(\pm\) 0.09 SE, \(n = 9\)) was used as the value for weight of seeds from 11 observations where no foraging had been observed at 1 tray of a pair, although the results of the analysis were the same if only values from foraged trays were used. Because of the complex structure of our statistical model and the unbalanced nature of the foraging data, we used the Satterthwaite approximation to determine the denominator degrees of freedom for our tests (Littell et al. 1996). Analyses were conducted with SAS version 8.1 (SAS Institute Inc. 2000); all *P* values are 2-tailed.

**Results**

**Rodent foraging.**—Examination of 193 foraging observations revealed no difference in overall seed removal in connected, rectangular, and winged patches (Table 1). A significant effect of location was found within each patch type (Table 1; Fig. 2). In connected patches, *P. polionotus* removed more seeds from the core of each patch than from the corridor (*t = −2.18, df. = 22.6, *P = 0.04*), with a similar, although less pronounced, trend at the core compared to the patch edge (*t = −1.95, df. = 22.1, *P = 0.06*; Fig. 2). Equivalent amounts of
seeds were removed from edge and corridor locations in connected patches ($t = 0.7, df = 22.5, P = 0.49$). In rectangular patches, seed removal did not differ between core and edge habitats ($t = -1.29, df = 24.5, P = 0.21$; Fig. 2). Seed removal in winged patches was greatest in the core compared to both the edge ($t = -2.18, df = 21.9, P = 0.04$; Fig. 2) and the wings ($t = -5.13, df = 21.8, P < 0.01$). Seed removal also was greater at the edge compared to the wings ($t = -3.80, df = 22.3, P < 0.01$). Overall, seed removal was greatest in sheltered microhabitats (Table 1). No interaction was found between patch type and tray microhabitat (Table 1), and no overall interaction was found between location and tray microhabitat (Table 1). However, planned contrasts revealed that, for the edge of connected and winged patches, seed removal was greater in sheltered trays (Table 1). In all other locations, no difference was found in foraging between sheltered and exposed microhabitats (Table 1).

Rodent abundance and activity.—In 312 trap nights, we captured 45 individuals representing 80 total captures. Forty-two *P. polionotus* (18 females and 24 males) were captured 73 times. One eastern harvest mouse (*Reithrodontomys humulis*) and 2 cotton mice also were captured. No movements of mice occurred among locations or patches. No difference was found in the number of *P. polionotus* ($M_{t+1}$) among patch types ($F = 0.45, df = 2, 6.41, P = 0.66$; Fig. 2) and no differences were found among locations within patch types ($F = 1.96, df = 5, 10.7, P = 0.17$). Although there was no main effect due to patch type, the number of *P. polionotus* was greater in the core compared to the corridor ($t = 3.04, df = 10.7, P = 0.01$; Fig. 2).

No difference was found in the activity of *P. polionotus* (as measured by total captures) among patch types ($F = 0.36, df = 2, 6.20, P = 0.71$; Fig. 2), but activity varied among locations within patch types ($F = 3.88, df = 5, 10.4, P = 0.03$; Fig. 2). Within connected patches, total captures were greater in the patch core compared to the edge ($t = 2.20, df = 10.4, P = 0.05$; Fig. 2), and to the corridor ($t = 3.85, df = 10.4, P < 0.01$). Activity in connected patches was not greater at the edge than in the corridor ($t = -1.65, df = 10.4, P = 0.13$). No difference was found in activity between the core and edge in rectangular patches ($t = 0.82, df = 10.4, P = 0.43$). Although marginally significant, there was a trend of less activity at the edge of winged patches compared to the core ($t = 1.94, df = 10.4, P = 0.08$). No difference was found in activity between edge and wing locations in winged patches ($t = -1.17, df = 10.4, P = 0.27$) or between core and wing locations ($t = -0.78, df = 10.4, P = 0.45$).

### Discussion

Examination of our results suggests that corridor-mediated changes in patch shape, not connectivity, affected within-patch foraging activity of *P. polionotus*, but did not affect abundance of *P. polionotus*. Proximity to edge was important in mediating risk-sensitive foraging behavior: in connected and winged patches where edges composed a greater amount of the patch, foraging near the edge was reduced. Although the difference in foraging between the edge and core of connected patches was marginally nonsignificant ($P = 0.06$), activity patterns revealed by live-trapping data offer strong support for greater activity of *P. polionotus* in the core compared to edge of connected patches (Fig. 2). In rectangular patches where the patch interior composed a greater relative amount of patch area, foraging and activity near edges resembled foraging in the patch interior (Fig. 2). *P. polionotus* is an old-field specialist (Davenport 1964), and the aversion to edge we detected is consistent with other studies: *P. polionotus* was more frequent in the center of patches (Mabry et al. 2003), and predation risk and foraging behavior are edge-specific for other *Peromyscus* species (Bowers and Dooley 1993; Morris and Davidson 2000; Wolf and Batzli 2004). Examination of our results also suggests that patch shape may have changed the strength of the edge effect on *P. polionotus* by changing the relative amount of edge in a patch. That is, the response of *P. polionotus* to edge was not solely a function of the distance to nearest edge, but was a function of several edges (Fagan et al. 1999; Ries et al. 2004), as supported by the decreasing difference between seed removal in core and edge locations as patch shape changed from winged to connected to rectangular (Fig. 2).

Seed removal patterns in wings and corridors also suggest edge-averse behavior by *P. polionotus*. In wings, where rodents were near 3 forest edges (Fig. 1), overall seed removal was

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### Table 1

Mixed-model analysis of variance examining the effect of patch type (connected, rectangular, or winged), location within each patch (core, edge, corridor, or wing), and tray microhabitat (sheltered or exposed) on the giving-up density (density at which the mouse had given up foraging) for *Peromyscus polionotus*. Giving-up density was measured as the weight of seeds remaining in a foraging tray. Denominator degrees of freedom were determined by using the Satterthwaite approximation (Littell et al. 1996). Interactions among location and tray microhabitat are dissected into linear contrasts to determine if the relationship between sheltered and exposed trays changes with location.

<table>
<thead>
<tr>
<th>Effect</th>
<th>df (numerator, denominator)</th>
<th>F ratio</th>
<th>P</th>
</tr>
</thead>
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<tr>
<td>Patch type</td>
<td>2, 6.72</td>
<td>0.32</td>
<td>0.73</td>
</tr>
<tr>
<td>Location (patch type)</td>
<td>5, 22.6</td>
<td>7.60</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Microhabitat</td>
<td>1, 15.9</td>
<td>5.14</td>
<td>&lt;0.01</td>
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<tr>
<td>Microhabitat × patch type</td>
<td>2, 16.1</td>
<td>1.60</td>
<td>0.23</td>
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<tr>
<td>Sheltered versus exposed, core (connected patch)</td>
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<td>0.01</td>
<td>0.95</td>
</tr>
<tr>
<td>Sheltered versus exposed, edge (connected patch)</td>
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<td>5.15</td>
<td>0.04</td>
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<td>0.18</td>
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<tr>
<td>Sheltered versus exposed, edge (rectangular patch)</td>
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<td>Sheltered versus exposed, core (winged patch)</td>
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<td>Sheltered versus exposed, wing (winged patch)</td>
<td>1, 17.3</td>
<td>0.03</td>
<td>0.86</td>
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lower than at the edge or core of the winged patch (the end of the wing forms the 3rd edge; Fig. 2). Corridors, in contrast, were only near 2 forest edges, and overall seed removal was similar to the edges of connected patches (Fig. 2). The low abundance and activity of *P. polionotus* in wings and corridors (Fig. 2) and the lack of difference between exposed and sheltered trays suggest that corridors and wings were simply risky places that are avoided regardless of microhabitat (i.e., risk within corridors and wings may override any protection afforded by sheltered microhabitat—Abramsky et al. 2002).

Examination of livetrapping data suggests that patch shape and connectivity had weak effects on the abundance of *P. polionotus* (Fig. 2), with the exception of a greater number of mice captured in the core of connected patches compared to the corridor (Fig. 2). Rather, the activity of *P. polionotus* shifted in a manner similar to foraging tray results. These findings are consistent with other studies that have shown nonexistent or variable impacts of corridors on abundance of *P. polionotus*, but consistent impacts of corridors on activity and behavior of *P. polionotus*. In a similar experimental system, Danielson and Hubbard (2000) found that abundance of *P. polionotus* was not affected by corridors, but that female *P. polionotus* exhibited greater patch residency times in connected patches. Mabry et al. (2003) found that abundance of *P. polionotus* in connected and unconnected patches did not differ for 2 years of the study, but was lower in connected patches during the 3rd year of the study.

Our findings provide additional evidence that activity and within-patch distribution of *P. polionotus* differs in connected patches (Mabry and Barrett 2003; Mabry et al. 2003), and suggest that this pattern is not a function of connectivity, but is rather a function of patch shape. Moreover, our work suggests that predation risk is the mechanism that drives this shift. Why would edges in rectangular patches be viewed as less risky from the perspective of *P. polionotus*? Reduced foraging by mice in exposed microhabitats near the edge of connected and winged patches may be because these patches provide more suitable habitat for edge-selecting predators, making edges in rectangular patches inherently less risky in comparison. Mammalian predators, such as skunks, red foxes, and raccoons, are more likely to enter and exit patches at patch corners compared to straight patch edges (Kuehl and Clark 2002). As such, connected and winged patches provide additional points of predator entry and exit not found in rectangular patches.

Examination of our results suggests that edge-mediated shifts in rodent impact (Bowers and Dooley 1993; Burkey 1993; Díaz et al. 1999; Manson et al. 1999; Nickel et al. 2003; Ostfeld et al. 1997) and behavior (Harper et al. 1993; Lidicker 1999; Wolf and Batzli 2004) may be a function of patch shape, and these located in the center of the patch (Core) and at the edge of the patch (Edge). Within connected patches, a foraging station also was located in the corridor (Corridor). Within winged patches, a foraging station was located in one of the wings (Wing). Values for giving-up density (remaining seeds) were cube-root transformed; values for abundance and activity were not transformed. Bars indicate mean ± 95% confidence intervals.

**FIG. 2.**—A) Seed removal, B) abundance of *Peromyscus polionotus* (calculated as $M_{n+1}$), and C) number of total captures of *P. polionotus* in an experimental landscape at the Savannah River Site, Aiken, South Carolina, in 3 different patch types: connected (CONN), rectangular (RECT), and winged. Within each patch, foraging stations were...
impacts may have consequences for plant recruitment (Orrock et al. 2003). Orrock et al. (2003) detected greater rates of seed predation by rodents in connected patches compared to winged and rectangular patches. Because Orrock et al. (2003) measured seed predation near the center of each patch, the increased seed predation they detected may have been due, at least in part, to greater levels of foraging in the interior of connected patches by *P. polionotus*. In long, linear patches, such edge avoidance by rodent seed predators could result in large areas that are relatively free of predation risk from the perspective of a seed. Because rodents are selective seed predators, changes in rodent foraging due to patch shape and connectivity could lead to shifts in plant community composition (Brown and Heske 1990).

To focus on patch shape and connectivity effects, we conducted our study over a short time period to reduce the potentially confounding effects of temporal changes in risk. However, temporal shifts in risk also are important in affecting rodent foraging, and these should be integrated with shape-mediated changes in risk in future work. For example, Bowers and Dooley (1993) found that seed removal, most likely by white-footed mice (*Peromyscus leucopus*), at the edges of grassland plots was lower on moonlit nights. Based upon our findings, the reduced foraging of *P. polionotus* during moonlit, rainless nights observed in other studies (Orrock et al. 2004) could interact with patch shape. In patches with relatively large amounts of edge (i.e., connected and winged patches), the difference in foraging between core and edge areas should be least on rainless nights or nights with little moonlight, although this has yet to be examined.

**Conclusions.**—Corridors affect movement, abundance, and behavior of many species (Beier and Noss 1998; Haddad et al. 2003; Rosenberg et al. 1997; Tewksbury et al. 2002). However, the impact of corridors on within-patch processes may be of equal or greater importance than the impact of corridors on between-patch processes. For species where adults rarely disperse, such as *P. polionotus*, corridor-mediated changes in patch colonization (Haddad et al. 2003), adult residency (Danielson and Hubbard 2000), and foraging behavior (Fig. 2) may have important consequences for long-term, landscape-level persistence and gene flow. Because preliminary studies suggest that *P. polionotus* may reside within the same patch for more than 2 years, within-patch foraging patterns shaped by patch geometry may shape the seed bank, with potential consequences for plant recruitment (Orrock et al. 2003) and community structure.

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**LITERATURE CITED**


MABRY, K. E., E. A. DREELIN, AND G. W. BARRETT. 2003. Influence of 
landscape elements on population densities and habitat use of three 
MANSON, R. H., R. S. OSTFELD, AND C. D. CANHAM. 1999. Responses 
of a small mammal community to heterogeneity along forest–old-
MECH, S. G., AND J. G. HALLETT. 2001. Evaluating the effectiveness of 
MORRIS, D. W., AND D. L. DAVIDSON. 2000. Optimally foraging mice 
match patch use with habitat differences in fitness. Ecology 81:
2061–2066.
habitat edges as refugia from microtine herbivory in tallgrass 
prairies. Oikos 100:525–533.
foraging is affected by indirect, but not direct, cues of predation 
Spatial ecology of predator–prey interactions: corridors and patch 
OSTFELD, R. S., R. H. MANSON, AND C. D. CANHAM. 1997. The effects of 
rodents on survival of tree seeds and seedlings invading oldfields. 
Ecology 78:1531–1542.
Ecological responses to habitat edges: mechanisms, models, and 
variability explained. Annual Review of Ecology, Evolution, and 
Systematics 35:491–522.
counts of individuals captured as indices of population size. Journal 
TEWKSBURY, J. J., ET AL. 2002. Corridors affect plants, animals, and 
their interactions in fragmented landscapes. Proceedings of the 
WOLF, M., AND G. BATZLI. 2004. Forest edge—high or low-quality 
habitat for white-footed mice (Peromyscus leucopus)? Ecology 
85:756–769.
River, New Jersey.
Associate Editor was Eric C. Hellgren.