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The influence of corridors on the movement behavior of individual *Peromyscus polionotus* in experimental landscapes

Brent J. Danielson* & Michael W. Hubbard
Department of Animal Ecology, 124 Science Hall II, Iowa State University, Ames, Iowa 50011-3221, USA;
(Corresponding author: Phone: 515-294-5248; Fax: 515-294-7874; e-mail: brent@iastate.edu)

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Abstract

To assess corridor effects on movement in *Peromyscus polionotus* (old-field mice), we used a set of three experimental landscapes that contained multiple patches (1.64 ha) of usable, open habitat embedded in a loblolly pine (*Pinus taeda*) forest matrix. Some patches were connected by corridors and others were isolated (unconnected). We introduced mice to nest boxes in experimental patches and followed them through the landscapes via trapping. We found weak evidence that the presence of corridors decreased the probability that *P. polionotus* (particularly females) would disperse or disappear from a patch. In the process of live trapping the patches, we also encountered 'feral' *P. polionotus*, *Sigmodon hispidus* (cotton rats), and *Peromyscus gossypinus* (cotton mice). The average number of feral animals did not differ between isolated and connected patches. This suggests that corridors do not act as drift fences that 'sieve' individuals out of the matrix and into the patches. However, more male than female *P. polionotus* and *S. hispidus* were trapped in isolated patches. This intersexual difference did not exist in connected patches.

Introduction

The importance of corridors to metapopulations in heterogeneous landscapes is well documented (e.g., Fahrig and Merriam 1985, 1994; Opdam 1988; Bennett 1990a, b; Henein and Merriam 1990; Merriam and Lanoue 1990; Bunce and Howard 1992; Taylor et al. 1993; Anderson and Danielson 1997). An abundance of studies demonstrates the effects of landscape features (esp. corridors) on population dynamics and, implicitly, on dispersal (e.g., Hansson 1987; Bennett 1990a; Bennett et al. 1994; Fahrig and Merriam 1985; Stamps et al. 1987; La Polla and Barrett 1993). However, little data exist on exactly how landscape features affect dispersal behavior at the level of the dispersing individual (but see Wiens et al. 1993). Empirical data show that patches connected by corridors have lower extinction rates, higher colonization rates, and greater population abundances (e.g., Wegner and Merriam 1979; Hansson 1987; Szzcki 1987; Bennett 1990b; La Polla and Barrett 1993; Bennett et al. 1994). However, the behavioral responses of individuals to landscape features such as corridors are not well known. Further, current trends in population modeling simulate individuals and, thus, must explicitly define how landscape features influence movement behavior.

Despite decades of research, relatively little is known about dispersal other than: (1) it tends to be density independent, (2) there are often age and sex biases amongst dispersers, and (3) a number of motivating factors may be ultimate evolutionary causes of dispersal (e.g., inbreeding avoidance, hierarchical social status, resource depletion, parasite avoidance; see Johnson and Gaines 1990; Stenseth and Lidicker 1992 for reviews). Thus, we know little about the actual dispersal process itself.

As a result of this lack of knowledge, most current Spatially Explicit Models (SEMs) use very crude and rather unrealistic algorithms for simulating the dispersal and site-selection processes. Often, disper-

sal algorithms and dispersal parameter estimates are derived from a 'best-fit' process that matches current distributions with the predictions from a series of model runs that use different sets of rules for dispersal behavior. While this validation process is not entirely circular, for the purpose of modeling population dynamics, a more robust method based on field data obviously would be preferred. Also, generalizing from sensitivity analyses (e.g., Pulliam et al. 1992) is difficult and may not be relevant to other models or ecological systems or species (Conroy et al. 1995; Dunning et al. 1995). For these reasons, a general set of realistic 'rules' (sensu Wiens et al. 1993) that governs the interactions between the individual and spatially heterogeneous landscapes is needed to allow the formulation of robust predictive models. The purpose of this study is to add to the current list of general rules concerning dispersal behavior as required by SEMs (Dunning et al. 1992, 1995).

In lieu of any definitive data, some widely cited models (e.g., Henein and Merriam 1990) simply assume that a fixed proportion of a resident population will disperse with or without corridors, while other models (e.g., RAMAS – Space; Akçakaya and Ferson 1990) assume that dispersal occurs only if corridors are present. There is a need to clarify the relationship between the presence and absence of corridors and the likelihood that an individual will disperse.

This study was intended to determine how individual animals (esp., *Peromyscus polionotus*) view potential corridors for dispersal. Specifically, we propose to answer three questions that are fundamental to understanding how corridors might be utilized by small mammals.

(i) Does the presence of a corridor increase the probability that an individual will disperse?
(ii) Does the presence of a corridor funnel a disproportionate fraction of the dispersers out of the resident patch and through the corridor, rather than dispersing in random directions?
(iii) Do corridors act as 'drift fences' that capture individuals dispersing through the matrix and funnel them into patches of usable habitat?

In the process of collecting data to answer the above questions, we also collected data on two other free-ranging species (*Sigmodon hispidus* and *P. gossypinus*) as well as free-ranging *P. polionotus* that dispersed to sites independently. We refer to these as 'feral' animals for the purposes of this study.

Methods

On the Savannah River Site (SRS) National Environmental Research Park, we used three sets (A1, A2, and A4) of experimental landscapes comprised of clearcuts surrounded by coniferous loblolly pine (*Pinus taeda*) forest (see Anderson 1995 for detailed description). These clearcuts and their associated systems of corridors were established by the United States Forest Service Savannah River Institute in 1994 and 1995 for the purpose of studying corridor effects on plant and animal dynamics. The square, 1.64-ha clearcuts are arranged in combinations of isolated patches and patches connected in couplets by 32-m wide clearcut corridors of similar habitat and varying lengths (128–384 m).

The A1 landscape contained 10 patches. Three corridors of 128 m, 256 m, and 384 m connected six of these patches in couplets (Figure 1). The A2 landscape contained 3 patches, two connected by a 256 m corridor and one isolated patch. The A4 landscape also contained 3 patches, two connected by a 128 m corridor and one isolated patch.

Of our three study species, *P. polionotus* and *S. hispidus* are open habitat and clearcut specialists, while *P. gossypinus* is less affiliated with these habitats (Anderson 1995; Danielson and Anderson 1999). Live trapping in SRS forest habitat in 1994 and 1995 yielded no *P. polionotus*, and only one *S. hispidus* (captured only one time), in 1500 trap nights of 10 mature forest stands (Anderson 1995). While sampling only ten stands may not represent a large sample of this particular habitat type, these stands (and trap locations within stands) were deliberately chosen because they appeared to have the best microhabitat conditions for these species. Thus, we feel confident that these species do not find forested habitat to be usable and only occur there for the purposes of passing through to other, better habitats.

Each patch was equipped with 18 subterranean nest boxes and 18 Sherman live traps uniformly dispersed within each patch. In 1995, nest boxes were made of standard, three-cavity, cement cinder-blocks ($20 \times 20 \times 40$ cm; King 1983). Each block had entrance and exit holes and a small passage cut between the cavities. Floors and ceilings were created with solid cement blocks ($3.5 \times 20 \times 40$ cm). The blocks were buried so their tops were level with the surface of the surrounding soil, and the top block could be easily removed to examine the nest box for animals.

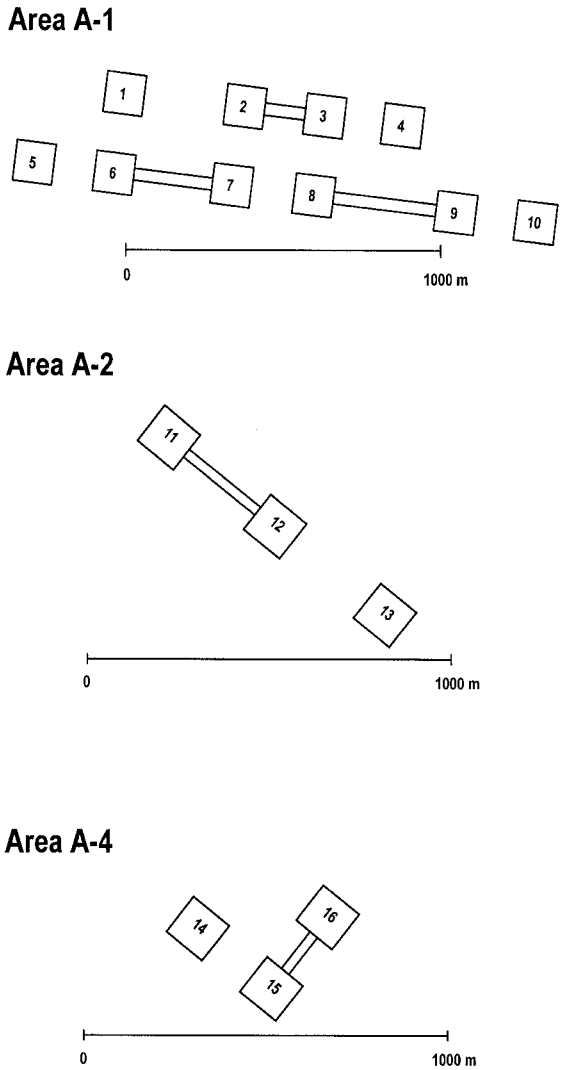

Figure 1. Three experimental landscapes on the Savannah River Site with 128 × 128 m clearcut patches (1.64 ha) and 32 m wide corridors of three lengths (128 m, 256 m, or 384 m in length) surrounded by loblolly pine forest.

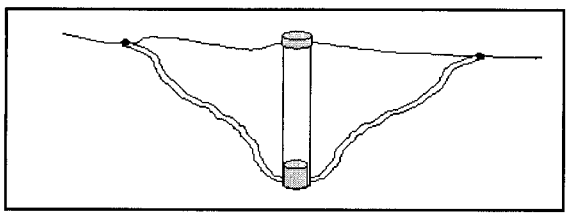

Figure 2. Nest-box apparatus used in 1996. The central shaft was constructed of PVC pipe, 0.10 m in diameter, and capped with a standard PVC pipe cap. The nest chamber was a wire-cloth (0.0125 m mesh) cage lowered to the bottom of the shaft at approximately 0.75 m below ground level. A pair of 0.025 m exit tunnels were constructed from flexible corrugated wire-harness sheathing and ran diagonally to the surface from the nest chamber.

Poor introduction success in 1995 was attributed to high interior nest-box temperatures. Although nest boxes were shaded with branches and locally obtained debris, interior temperatures often exceeded 40 °C. Thus, in 1996, all cinder-block nest boxes were replaced with more elaborate nest chambers (Figure 2) that more closely mimicked natural *P. polionotus* nests (Michael Smith pers. comm.). These chambers consisted of a 0.75 m length of PVC drain pipe approximately 0.1 m in diameter. The pipe was buried vertically and flush with the surface of the ground. A nest chamber made of 0.0125 m hardware cloth was constructed to loosely fit the inside diameter of the pipe. This chamber was approximately 0.12 m tall with a pair of 0.025 m squares cut through its sides. When the nest chamber was fully inserted into the pipe, these holes aligned with corrugated plastic tubes (approximately 1.2 m long and 0.025 m diameter) that extended diagonally to the soil surface. The nest-box pipe was fitted with a removable cap. Nest chambers were supplied with cotton batting for nest material, whole oats for food, and potato or apple pieces for moisture. The 1996 nest-box design maintained cooler temperatures than cinder-block nest boxes.

We introduced *P. polionotus* into the nest boxes throughout the summers of 1995 and 1996. Because we used wild-caught mice, they were introduced as they became available through trapping at off-site locations. In 1995, we introduced mice only into the A1 landscape, while in 1996, we used each of the three landscapes more equitably.

We used the same introduction procedure in each field season. Mice were live trapped at many locations scattered throughout the SRS, at least 1 km from our experimental patches. These mice were placed in nest boxes in patches with and without corridors. Upon introducing a mouse to a nest box, wire-cloth tubes approximately 0.025 × 0.25 m were attached to the two entrances of the burrow system. These tubes prevented the mice from leaving the boxes and allowed them to come above ground and experience the local environment. After 3 days, the tubes were removed and the mice were free to move. The 3-day waiting period was intended to allow the animals to become familiar with the nest boxes and eventually rear offspring in them. All introduced mice were treated similarly and, to the extent that dispersal from the patch of introduction represents an attempt to return to their original home ranges, all treatments patches (isolated and connected) were similarly affected. Both dispersal and homing from our experimental patches represent the

behaviors of individuals moving through unfamiliar territory. Thus, even if the movements by these mice represent homing, we can assume that their behaviors in this unfamiliar landscape are similar to those of truly dispersing mice (Stickel 1968).

Upon release, many mice simply disappeared or were rarely found in nest boxes. Reproduction did occasionally occur in nest boxes, but usually during the 3-day introduction period. These litters were removed by the female when the box was opened, or they died due to predation by fire ants. Because we obtained very few juveniles reared by known mothers at known natal nest sites, we have focused our analyses on the movement of the introduced adult animals.

We ear tagged all introduced *P. polionotus* prior to their release and all juveniles that were born to introduced mice prior to their becoming independent (approximately 17–19 days of age). Thus, we were able to determine the origin of any individual that moved between patches in the experimental landscape.

We categorized the fates of introduced mice as *known nondispersers*, *known dispersers*, or *disappeared* (either dead in situ or dispersed but not recorded elsewhere, see below). The *known dispersers* class was composed of individuals that left the patch in which they were introduced within 2 weeks of being released from the nest box. Past research has shown that the 2-week interval is long enough for an individual to sample a patch of habitat and either settle into a home range or leave (Danielson and Gaines 1987; Danielson and Swihart 1987). These animals were known to have dispersed because they were recorded in a nest box or trap in another patch within that time interval.

Introduced animals that stayed (*known nondispersers*) were animals that were observed in nest boxes or traps in the patch in which they were introduced at least 2 weeks after being released. Finally, animals that *disappeared*, were animals that were never seen in any patch 2 weeks after being released.

We hypothesized that, if corridors act to encourage individuals to disperse, a greater number of individuals introduced into patches with corridors would disappear than would be the case for individuals introduced to isolated patches. If dispersers strike out in random directions from where they were introduced, we would expect, based on the proportion of the edge of the patch that contacts the corridor, about 1/16th of the dispersers from a patch should travel the corridor to the unoccupied patch. If, on the other hand, corridors act to funnel a disproportionate number of dispersers (objective (ii) above), the number of animals that travel through the corridor will exceed 1/16th of all dispersers. We cannot estimate the number of animals that made use of the corridors by sampling the unoccupied patch in each couplet because animals that leave via a corridor may not stop once they reach the patch at the other end. Furthermore, equating disappearance from a patch with dispersal, biases the disappearance data with unrecorded patch mortality. Such a bias would act to make tests conservative, but lack power (i.e., high probability of Type II error).

To identify those animals that left the patch to which they were introduced, we live trapped all patches in A1 in 1995 and in A1, A2, and A4 in 1996, on a biweekly basis, using 18 Sherman live traps in each patch. All introduced *P. polionotus* were recorded and released. 'Feral' *P. polionotus* that colonized the patches on their own were recorded and removed from the landscapes, and all *P. gossypinus* and *S. hispidus* were ear tagged and released where they were captured. At the same time, all nest boxes were checked for use and these data were included with the live trapping data. These data were used to assess the fates of introduced animals and the effectiveness of the corridors in capturing other individuals that may have been dispersing through the matrix.

Results

Fates of introduced P. polionotus

A total of 285 *P. polionotus* was released into 9 of the 16 patches (3 isolated and 6 connected patched). Of these, 69 animals were classified as *known dispersers*, 91 as know nondispersers, and 125 animals disappeared (Table 1).

When data were combined across years, no differences in the frequencies of the three classes were observed among isolated and connected patches ($\chi^2 = 0.870$, $P = 0.647$). Separate analyses of the 1995 and 1996 data also showed no differences ($\chi^2 = 4.234$, $P = 0.120$ and $\chi^2 = 2.999$, $P = 0.223$, respectively). Therefore, for further analysis, we combined data across years.

Since male and female mammals are known to have different dispersal strategies, we also analyzed data by gender. When *known dispersers* and *disappeared* classes were combined and each gender was analyzed separately, the presence or absence of corridors still did not affect the probability that an individual would remain in a patch (males, $\chi^2 = 0.096$, $P =$

Table 1. The number of *P. polionotus* introduced to experimental patches (1995 and 1996 combined). Each release patch was either connected to another similar patch or isolated by at least 128 m of mature pine forest from all other suitable habitat. Animals known to have dispersed left the patches where they were released and were caught in another patch. Animals known to have stayed remained in the patches in which they were released for at least 14 days. Animals that disappeared were never seen after the first 14 days of their release. They may have dispersed from the region or died *in situ*.

Release patch	Connected or isolated	Number Released	Number known dispersers	Number known nondispersers	Number disappeared
1	Isolated	65	16	20	29
2	Connected	1	0	1	0
3	Connected	75	17	18	40
6	Connected	1	0	1	0
7	Connected	34	14	11	9
10	Isolated	21	3	7	11
12	Connected	21	5	11	5
14	Isolated	26	5	9	12
15	Connected	41	9	13	19
Totals		285	69	91	125

0.756; females, $\chi^2 = 0.169$, $P = 0.681$). However, when isolated and connected patches were combined, more females tended to disperse or disappear, whereas males tended to stay in the patch in which they were introduced ($\chi^2 = 2.806$, $P = 0.094$).

To more clearly define the effect of corridors, gender, and other factors that may influence an individual's decision to stay or disperse, we performed a multivariate logistic regression on the probability of an individual's staying versus the combined probability of dispersing or disappearing with the presence or absence of corridors, gender, and the number of individuals simultaneously released in the patch. A significant multivariate logistic regression ($P = 0.0003$) was obtained in which two variables, gender and the number of animals simultaneously released, were strongly significant ($P = 0.0163$, $P = 0.0003$, respectively). Other variables considered during model development included patch identifier, release date, total released in each patch in each year, and presence or absence of a corridor. These variables were not significant. However, the variable indicating the presence or absence of corridors approached significance ($P = 0.0713$). The model revealed that females were more likely than males to disperse or disappear from the patch of introduction, which is consistent with the χ^2 test above. Furthermore, the probability of leaving the patch of introduction was positively related to the number of individuals released in the same patch at the same time. Finally, to the extent that the corridor variable was significant to the model, the probability that an individual would disperse or disappear was *negatively* related to the presence of a corridor.

Distribution of feral mice

Given that corridors may act to filter dispersing animals from the matrix and funnel them into suitable habitat patches, we expected to catch more feral mice from patches with corridors. Because trapping effort was equivalent in isolated and connected patches, we summed the number of feral *P. polionotus*, *P. gossypinus*, and *S. hispidus* captured in each patch (Table 2). In general, isolated patches and patches connected to corridors were colonized by similar numbers of feral individuals of all species (t-test, $P > 0.4$).

Since mammals generally display sex-biased dispersal and male movements are often the result of mate-searching behavior (Johnson and Gaines 1990), we analyzed feral captures by gender. For *P. polionotus* and *S. hispidus*, we found that males were captured more often than females in isolated patches (t-test, $P = 0.0056$ and $P = 0.0569$, respectively). No differences were observed between sexes for *P. gossypinus* in isolated patches or between genders of all three species in connected patches.

Table 2. The number of feral *P. polionotus*, *P. gossypinus*, and *S. hispidus* that were captured in patches with corridors and isolated patches. Where the numbers of males and females add to less than the 'Total' number, gender of some animals was not recorded.

Patch number	*P. polionotus*			*P. gossypinus*			*S. hispidus*		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
Isolated patches									
1	6	2	8	13	10	27	6	1	7
4	8	2	12	11	5	16	5	0	5
5	7	4	16	15	11	29	3	0	3
10	4	4	8	6	6	15	1	1	2
13	6	5	11	0	0	0	0	0	0
14	5	3	8	10	6	16	2	1	3
Mean	6.00	3.33	10.50	9.17	6.33	17.17	2.83	0.50	3.33
Variance	2.00	1.47	10.30	29.37	15.47	107.77	5.37	0.30	5.87
Connected patches									
2	5	8	13	14	10	25	5	8	13
3	2	3	5	8	7	17	3	2	5
6	4	8	12	12	11	23	2	4	6
7	4	5	9	8	4	12	0	2	2
8	4	7	12	11	6	17	1	4	6
9	9	7	16	1	1	2	4	3	7
11	9	6	16	8	2	11	3	4	7
12	4	2	7	5	2	7	0	0	0
15	4	3	9	4	4	8	1	0	1
16	2	3	6	6	7	13	0	0	0
Mean	4.70	5.20	10.50	7.70	5.40	13.50	1.90	2.70	4.70
Variance	6.01	5.29	15.39	15.34	11.60	51.17	3.21	6.23	16.46

Discussion

The fates of introduced *P. polionotus* appeared to be little affected by the presence of corridors connected to the patches in which they were introduced. In fact, if anything, corridors seemed to reduce, rather than increase the probability that an animal would leave. This counterintuitive result might be explained as an area effect. From the perspective of a mouse, patches on the SRS with corridors may simply be larger patches, and thus, patches with corridors represent greater amounts of habitat available to the introduced individual. Therefore, a mouse introduced into a patch with a corridor may be less likely to leave. This is consistent with the suggestion that intraspecific competition for space might be stronger in potentially smaller patches. The positive relation between the number of conspecifics introduced and the number of individuals which dispersed or disappeared may be further evidence of this relationship. The stronger relationship observed for females is consistent with the generally stronger territoriality between females than between males for other members of the genus *Peromyscus* (e.g., Wolfe et al. 1983, Wolfe 1993, Halama and Dueser 1994, Wolfe and Peterson 1998).

Our data do not suggest that *P. polionotus* which leave do so by moving down existing corridors more than through the timber. Using the same experimental landscapes, Bowne et al. (1999) also found that corridors do not induce *S. hispidus* to leave patches. However, Bowne et al. did find that corridors are the preferred route of exit, if they do choose to disperse.

The drift-fence effect

Our data do not suggest that corridors cause a significant 'drift-fence effect'. Forman (1995) and Dramstad et al. (1996) suggested that corridors may serve to filter individuals from the inhospitable matrix habitat and funnel dispersers into patches. Modeling this effect of corridors has shown that it may affect the

size and the longevity of entire metapopulations (Anderson and Danielson 1997; Danielson unpublished). The reduction in metapopulation size and longevity in isolated patches may be the result of inequities in immigration that occur when isolated patches are shadowed by a corridor-patch complex and, thus, receive fewer dispersers than they might otherwise receive. Although Haddad and Baum (1999) have suggested that the drift-fence effect may occur for some species of open-habitat butterflies on the same study area in which we conducted these experiments, we found no evidence of greater numbers of the rodent species studied appearing in patches with corridors as opposed to isolated patches.

We did find that more feral male than feral female *P. polionotus* and *S. hispidus* were captured in isolated patches. This suggests that males are ranging more widely, presumably to find females with whom to mate, and is consistent with the general pattern of male-biased dispersal in mammals (Johnson and Gaines 1990). Alternatively, males may be more frequently excluded from connected patches by other adult males, however, a mechanism that would lead to differences between the two types of patches is unclear.

Unlike *P. polionotus* and *S. hispidus*, the number of feral *P. gossypinus* in isolated patches was not male biased. One possible explanation for this apparent contradiction is that *P. gossypinus*, may not perceive our experimental landscapes as fragmented, and, in fact, may be resident in the matrix timber surrounding the patches. If so, it may be no more difficult for relatively sedentary females to find our 'isolated' patches than it is for more widely ranging males. In fact, other data for this species on the SRS suggests that the species is not an open-habitat specialist, such as *P. polionotus* and *S. hispidus* (Anderson 1995; Golley et al. 1965).

The issue of scale

Our experiments may have been performed at an inappropriate scale. Very narrow corridors (2 m) connected to small patches have been shown to be very important to the movements of individual microtines and the configurations of their home ranges (Andreassen et al. 1998, Ims 1995, La Polla and Barrett 1993). The wide corridors (32 m) in this study may represent reasonable patches of useable habitat rather than potential pathways for dispersing *P. polionotus*. Home-range size for this species is on the order of 0.34 ha on the SRS (Davenport 1964) or approximately equivalent to the area of the shortest corridors (0.41 ha). Additionally, the inter-patch distances may be too short to be significant to these species. An earlier study of the small mammals in 196 clearcuts across the entire SRS showed that the presence of corridors, in the form of utility rights-of-way, within 250, 500, or 750 m of the sampled clearcuts are not significant predictors of the presence or absence of any of the three species included in this study (Anderson and Danielson in review; Anderson 1995).

The effect of corridors on metapopulations may be more important at much larger scales, where the flow of individuals over many generations regulates distributions and abundances over large regions (potentially much larger than the SRS). While utility rights-of-way are often very similar in width to our experimental corridors, they run for kilometers and have the potential to connect regions such as the SRS with similar national forests and other clearcut complexes that are inhabited by these species.

Conclusions

This study did not find a strong effect of corridors on the movements of *P. polionotus* that were introduced in patches that were connected to potential dispersal corridors. Corridors appear to have little effect on influencing an individual's decision to disperse. In fact, males appear more often than females in unconnected (isolated) patches, suggesting that they are less inhibited by the intervening matrix habitat. Also, the probability of a female dispersing was lower in patches which were connected to corridors. This effect was counter to our initial expectation, and it reflects the effect of a confounding variable – the availability of suitable habitat – if corridors are viewed as simply additional habitat usable for the establishment of a home range.

Corridors on the SRS do not seem to direct individuals that disperse by funneling them in the direction of other patches of usable habitat. Nor do they appear to act as drift fences to sift dispersing individuals out of the matrix and into the patches. These 'nonresponses' to corridors, if incorporated into spatially explicit models, would drastically alter their results. For example, a series of models by Anderson and Danielson (1997), Henein and Merriam (1990), Lefkovitch and Fahrig (1985) attempt to assess the importance of corridors to metapopulation size, persistence, and the distributions of abundances among patches. To the ex-

tent that these models are attempts to draw general conclusions about the utility of corridors, their results are highly suspect relative to their being applied to specific species. It is similarly easy to make these criticisms of many other SEMs, and thus, our data illustrates the need to actually measure these behaviors in the field for a variety of species in order that basic behavioral responses (or 'nonresponses') to corridors can be determined.

While we can provide no evidence in support of the hypothesis that corridors are beneficial to these wildlife populations in the short term, we recommend that further studies explicitly attempt to separate the confounding variable of availability of usable habitat from the presence of a true corridor effect. We know of no study of vertebrates that looks for an effect of corridors at scales so large that individuals that begin the dispersal process along the corridor are the ancestors of those which eventually arrive at a distant patch. Thus, we suggest that future studies address the effects of corridors over spatial scales at least 2 orders of magnitude greater than that of these experiments.

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