



Effects of landscape spatial structure on movement patterns of the hispid cotton rat (*Sigmodon hispidus*)

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Abstract

A large-scale experimental landscape study was conducted to examine the use of corridors and the forest matrix habitat by the hispid cotton rat (*Sigmodon hispidus*). The role of micro-habitat selection by *S. hispidus* in influencing routes of movement was also investigated. The experimental landscape consisted of ten 1.64-ha patches (each 128 × 128 m) established in a loblolly (*Pinus taeda*) forest. Four of the patches were isolated while the other six were connected in pairs by a 32-m wide corridor. Cotton rats ($N = 96$) were simultaneously released into both an isolated and connected patch, and monitored by radiotelemetry for 10 days. We found that the forest matrix was not a barrier to movements of cotton rats. Fifty percent of the cotton rats moved through the matrix. Corridors had no significant effect on the number of animals leaving connected patches (60%) compared to isolated patches (50%). However, corridors were the preferred route to leave a connected patch. Colonization success for cotton rats leaving connected and isolated patches did not significantly differ. Cotton rats exhibited micro-habitat preferences and these preferences differed within patch/corridor and matrix habitats. In patch/corridor habitats, cotton rats selected sites with tall (>1 m) shrubs and high percent cover. In the forest matrix, cotton rats selected sites with abundant cover by vines and low tree canopy cover. Movement patterns of *Sigmodon hispidus* are not strongly influenced by large-scale landscape spatial structures. Micro-habitat selection, however, does influence movement patterns. These findings have important implications regarding habitat connectivity for small mammals.

Introduction

The movements of small mammals in fragmented landscapes have received increased attention in recent years (Merriam and Lanoue 1990; Szacki and Liro 1991; Kozakiewicz et al. 1993). Most of this research has focused on quantifying movements between habitat patches to assess the degree of population isolation. Once the degree of isolation is determined, management strategies can be devised to minimize isolation by increasing connectivity. Connectivity is defined as the probability of movement between landscape elements (Merriam 1995). Corridors are one method to increase connectivity. Despite the perceived importance of corridors (Noss 1987), investigators have only recently focused on the actual use of corridors by

small mammals (Lorenz and Barrett 1990; Merriam and Lanoue 1990; La Polla and Barrett 1993). The importance of corridors will depend on the ecology and behavior of a species, and on the nature of the surrounding matrix.

The matrix is the most spatially dominant feature of a landscape (Forman 1995). If an animal is unable to move through the matrix, it will be restricted to isolated patches which frequently represent a very small portion of the total landscape. Populations in such isolated patches are at greater risk of extinction because of stochastic events (Fahrig and Merriam 1994). Population persistence may increase if movements between patches compensate for local demographic variability (Roff 1974; Hansson 1991). Hence, it is vital to know if a species in question is able to move through

the matrix. This ability will partially be determined by the characteristics of the surrounding habitat matrix. The matrix is expected to affect animals in a species-specific manner. The matrix functions as a filter, allowing some species to move through it while inhibiting others (Kozakiewicz 1993). The degree of movement will depend on the spatial structure (i.e., shape, size, and quality) of the landscape matrix, and on the ecology and behavior of a particular organism. Thus, there is need to better understand how movement patterns of a particular species are affected by landscape spatial structure.

The most detailed information on the movements of small mammals has come from research on activity within home ranges (Szacki and Liro 1991; Szacki et al. 1993; Collins and Barrett 1997). These investigations suggested that small mammal movements are minimal. However, much of this research may be biased due to the spatial limitations of live-trapping grids (Weigert and Mayenschiein 1966; Briese and Smith 1974; Banks et al. 1975; Andrzejewski and Babinska-Werka 1986; Szacki and Liro 1991; Szacki et al. 1993). Data on the distances of other types of movements (i.e., dispersal, exploratory) have been very difficult to acquire (Porter and Dooley 1993). Nevertheless, investigations have suggested that distances moved by small mammals during dispersal or exploratory movements may be even greater than generally believed, and that long-distance movements may be common (Crawley 1969; Furrer 1973; Clark et al. 1988; Szacki and Liro 1991; Kozakiewicz et al. 1993; Szacki et al. 1993).

While evidence for long-distance movements exists for small mammals, little is known about the rate, route, distance and direction of those movements (Szacki and Liro 1991; Szacki et al. 1993). In trap lines covering several habitats, Szacki et al. (1993) found that trap success corresponded with differences in habitat structure and interpreted this finding as indicating distinct routes of movement. If such routes exist, then individuals may be cueing in on particular vegetative or cover types. Vegetation or structural preferences have been demonstrated for several small mammal species (Lorenz and Barrett 1990; Merriam and Lanoue 1990; Bennett et al. 1994; Ruefenacht and Knight 1995). Thus, microhabitat heterogeneity within seemingly homogenous habitats may affect patterns of movement.

We investigated the use of landscape elements (i.e., patches, corridors, matrix) and microhabitat features by the hispid cotton rat (*Sigmodon hispidus*). The ex-

perimental landscape consisted of clear-cut patches that were either isolated or connected in pairs by a corridor. The matrix was a managed mature pine forest dominated by loblolly pine (*Pinus taeda*). We hypothesized that interpatch movements by cotton rats should not be restricted in isolated patches (i.e., the forest matrix should not serve as a barrier to movements). Alternatively, movements between isolated patches should be restricted and movements between connected patches should be facilitated by a corridor. Acceptance of the null hypothesis generates several predictions which are: (1) movement from a patch does not depend on the degree of isolation of the patch (i.e., corridors do not affect movement); (2) animals leaving isolated and connected patches will be equally successful in colonizing another patch; (3) net distances traveled by cotton rats released into isolated and connected patches will not differ significantly; and (4) movements by cotton rats are associated with particular vegetation types. Testing this hypothesis and verifying the predictions will provide insight into how small mammals perceive and use the landscape.

Material and methods

Study site

The study was conducted in an experimental landscape established at the Savannah River Site (SRS) in Aiken County, South Carolina, USA. The study area consisted of ten 1.64-ha patches (each 128 × 128 m) established in a loblolly pine (*Pinus taeda*) forest (Figure 1). Four of these patches were isolated whereas the other six were connected in pairs by a 32-m wide corridor. Corridor lengths were either 128, 256 or 384 m. Patches and corridors were oriented east to west and were established in February-March 1994 by standard U.S. Forest Service-Savannah River Site silvicultural practices (Haddad 1997). All trees within the designated patch and corridor boundaries were harvested. Patches and corridors were burned between November 1994 and February 1995. A 4 × 4 grid of markers (PVC poles) 32 m apart and 16 m from the edge was established within each patch. Markers were also linearly arranged in each corridor at 32-m intervals. East-west transects were established every 64 m in the forest matrix with markers placed along each transect at 32-m intervals.

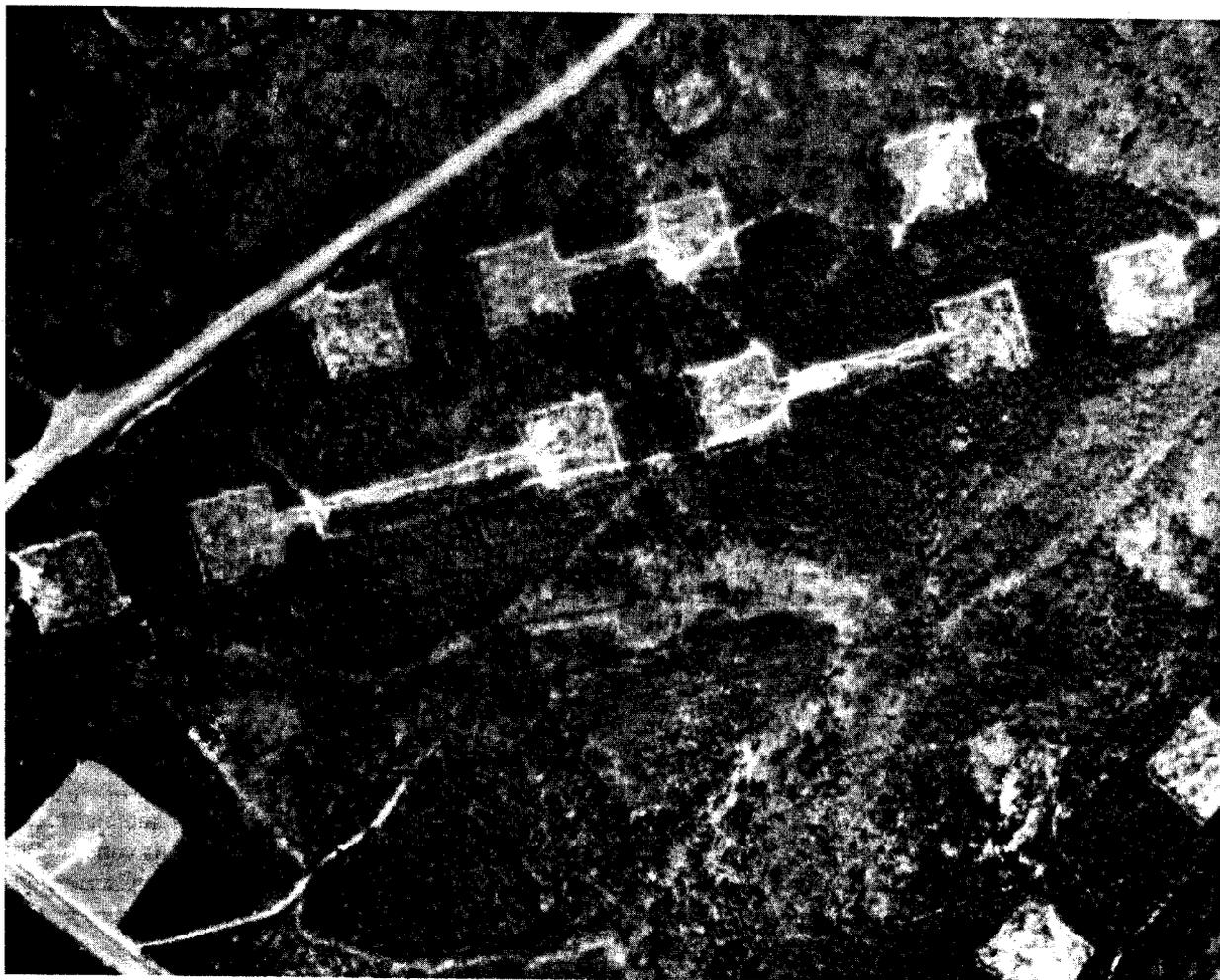


Figure 1. Aerial photograph depicting experimental landscape at the Savannah River Site. Each patch is 128×128 m.

Study species

Cotton rats have been shown to prefer grassland and old-field habitats (Cameron and Spencer 1981), but are generally considered a habitat generalist (Lidicker et al. 1992). Cotton rats are most often found in areas with a high herbaceous cover of perennial grasses of moderate to heavy density (Stokes 1995). At SRS, cotton rats are common residents of early-successional clear-cuts. Cotton rats supposedly shun areas where tree canopy shades ground cover (Geertz 1964). As such, they are not commonly found in forested areas. Several investigations have demonstrated that cotton rats exhibit differential microhabitat utilization (Odum 1955; Geertz 1964; Spencer and Cameron 1983; Kincaid and Cameron 1985; Lidicker et al. 1992). Importantly, this fine-scale vegetation selection may affect patterns of movement in this species.

Periods of release

Adult cotton rats (*Sigmodon hispidus*) were captured in old-fields on the SRS at a minimum distance of 13.4 km from the experimental study area. Translocated animals were used to mimic transients (Merriam and Lanoue 1990). Transients were expected to be more likely to move because of the absence of a home range. Captured animals were housed in Nalgene® cages for up to one month and fed a mixture of rabbit chow and sunflowers seeds. Twelve adult cotton rats (>90 g; 6 males, 6 females) were selected for each period of release. Each cotton rat was anesthetized with Metofane® (Mallinckrodt Veterinary, Inc. Mundelein, Illinois) and fitted with a BR collar containing a SM1-H transmitter with a loop antennae (4.5 g, AVM Instrument Co., Livermore, California). Each individual was allowed approximately 20 h to acclimate to the

collar before being released. Collars did not noticeably affect behavior while in captivity.

A total of 12 adult animals were tracked by radiotelemetry during each period of release. Dates of release coincided with the following seasons: early summer (24 May and 7 June), late summer (23 July and 6 August), early fall (14 September and 29 September), and late fall (2 November and 14 November) of 1996. A randomly-selected connected patch and a randomly-selected isolated patch were used in each release period. Although resident animals were rare, live-traps were set within each patch to remove resident cotton rats. Six animals (3 males, 3 females) were released at 0730 h into the center of both patches. At 0800 h and subsequently every four hours for the next 68 h, the location of each individual was determined by triangulation. After the initial 68 h, each individual was located twice in the evening at 4-h intervals for an additional seven days. Locations were recorded every four hours to minimize autocorrelation (Swihart and Slade 1985). Thus, each cotton rat was monitored for ten consecutive days.

Cotton rats were located with either a R2100 (Advanced Telemetry Systems Inc., Isanti, Minnesota) or a LA12-Q (AVM Instrument Co., Livermore, California) receiver with a three-element yagi antenna. Field markers established in each patch and corridor served as fixed points from which to triangulate. Test trials indicated locations were accurate to within 4.6 m. An animal's location within the forest was determined by homing (White and Garrott 1990) to within several meters. Experimental animals were recaptured at the conclusion of the release period by saturating the area with traps around the last documented location.

Vegetation sampling

Vegetation was sampled following each period of release at both documented locations of cotton rat movement and at random sites within the patches, corridors, and matrix. These samples were used to quantify habitat selection by cotton rats, as well as to quantify the quality of patches, corridors, and forest matrix. Vegetation was sampled within a patch at five randomly-selected sites where each animal was located. Characteristics of available habitat were determined at 32 random sites within each patch. A 16-m² quadrat oriented to the cardinal directions was established for each sample point. Within this quadrat, percent cover of shrubs, grasses, forbs, vines, total vegetation, and woody debris were visually estimated

and assigned a rank using a modified Braun-Blanquet scale (Kent and Cocker 1992): (0) <1%; (1) 1–5%; (2) 6–15%; (3) 16–25%; (4) 26–50%; (5) 51–75%; (6) 76–100%. The above scales were also used to determine percent cover of shrubs and herbaceous vegetation (grasses and forbs) for each height class. Height of shrubs were divided into four classes: ≥ 0.5 m, >0.5 to ≤ 1.0 m, >1.0 to ≤ 1.5 m, and > 1.5 m. The height of herbaceous vegetation (grasses and forbs) were grouped together into the following classes: <0.25 m, >0.25 to <0.5 m, and >0.5 m.

In addition to the above measurements, the number of trees were counted and densiometer readings were taken in forest quadrats. Densiometer readings were used to quantify tree canopy cover. Characteristics of vegetation at the site where each cotton rat was located were also determined in the forest matrix. Characteristics of available habitat were determined at 87 randomly-selected sites in the forest matrix during September and October 1996.

Data analyses

Two types of treatments were used in this study. The isolated-patch treatment ($n = 4$) consisted of patches that were not connected to another patch. The connected-patch treatment ($n = 6$) consisted of patches connected to one other patch by a corridor (Figure 1). Unless otherwise noted, data were pooled over all periods of release.

Movement from patches of release

An animal was considered to have left a patch when at least one location for that animal was determined outside of the patch. An animal was considered to have exited a patch via a corridor when the first location of that animal outside of a patch was in a corridor. To investigate the effects of corridors on the number of animals leaving a patch, a chi-square test for independence was performed using a 2×2 contingency table; rows indicated treatment type and columns indicated whether the animals remained or left the patch of release. Within a treatment type, a chi-square test for independence was also performed to test for differences in sex ratios of animals leaving a patch; rows indicated gender and columns indicated whether the animal remained or left the patch of release. A z-statistic (Zar 1984) was used to test the hypothesis that the proportion of animals leaving a patch via a corridor is equal to the percentage of the perimeter encompassed by the corridor (0.06). This analysis was

used to determine if corridors were the preferred route of movement from a patch.

The length of time until an animal moved from a patch was analyzed with the SAS procedure LIFETEST (SAS Institute, version 6.0). This nonparametric procedure compares survival curves between treatment type and gender. Leaving the patch was considered an analog of mortality and remaining in the patch was an analog of survival. Other events such as death, loss of transmitter, or a missing animal were treated as censored events when using this procedure. Censored events and individuals remaining in the release patch were recorded as the animal's last known location. The time when an animal was first located outside of the patch was recorded as an observed event.

Colonization success

The probability of an animal successfully finding another patch (i.e., colonization) was calculated as the angle subtended by that patch in relation to the center of the release patch divided by 360 degrees (Fahrig and Paloheimo 1988). The subtended angles were then summed for each release patch to compute the expected probability of colonization success for animals leaving the patch. A chi-square goodness-of-fit test was performed to compare observed frequency of colonization from a treatment type to the expected frequency for that treatment. This analysis assumed that the animals were naïve, the matrix was uniform, that no landscape feature directed movements (i.e., that corridors did not increase frequency of movements), and that animals did not significantly change direction while moving. The fourth assumption is supported by theoretical evidence (Dusenbery 1989). Success of colonization was tested for the first colonization event only because subsequent events would be influenced by the experiences of the cotton rats as they traversed the landscape.

Net distance moved

Net distance moved by each cotton rat was calculated as the straight line distance from the animal's location of release to the last known location. Net distances moved were analyzed at the end of ten days following release using an analysis of variance (ANOVA) for sex and treatment, and sex by treatment interaction blocked by release. In order to test for seasonal effects, variation among releases was partitioned into terms for season and release within season.

Daily patterns of activity

Distances moved during specific time periods (0800–1200, 1201–1600, 1601–2000, 2001–2400, 0001–0400, 0401–0800 h) were determined for each animal for the first 68 hrs following release. A repeated measures ANOVA was used to test for differences between gender, dates of release, and treatment. Missing values were predicted with a general linear model. On average, a prediction of distance moved per time period was calculated $5.3 (\pm 3.9 \text{ STD})$ times for each animal. Any negative values predicted were assumed to be zero to better reflect biological reality. A normalizing transformation was not needed because a plot of the residuals indicated a symmetrical distribution.

Direction of movement

To test for direction of movement, the angle from the center of each patch of release to an individual's location at the end of the ten-day study period was calculated. The Rayleigh test was used to determine if these points of location were uniformly distributed around a circle (Zar 1984). A separate Rayleigh test was performed to compare between treatments for animals that departed from the patch of release.

Characteristics of vegetation

Vegetation structure from randomly-selected sites was compared with the vegetation at sites where cotton rats were located to determine if cotton rats selected vegetation differently from what was available. Patch and corridor samples were grouped together for this analysis because they were of the same habitat type. Forest data were analyzed separately.

Vegetation data were analyzed using a mixed linear model in the SAS procedure MIXED (SAS version 6.12). The model was

$$y_{ijrlm} = \mu + \beta_r + t_i + \alpha_j + (t\alpha)_{ij} + e_{ijrlm},$$

where i is the class (vegetation structure at site where a cotton rat was located or at random sites within landscape elements), j is the vegetation type (shrub, grass, forb, or vine), r is the match between the location of the cotton rat and the appropriate patch, l is the replication over time (for successive cotton rat locations) or space (for random vegetation samples), and m is an identification number. The parameter μ is the overall mean, β_r is the patch effect, t_i is the class effect, and α_j is the variable effect. The mixed linear model accounted for correlation between successive locations

of the same individual and for vegetation samples within a given patch. The assumptions were that observations within classes were equally correlated with one another and that observations for different animals within a release patch were independent. Vegetation type and patches were treated as fixed effects. The centroid of each vegetation scale was used in the analysis to reduce the number of model parameters.

Results

Movements from patch of release and corridor use

No significant differences were found between isolated and connected patches regarding the number of cotton rats leaving a release patch ($X^2 = 1.13$, $df = 1$, $P = 0.29$). In isolated patches, 14 cotton rats (29.2%) stayed, 24 (50.0%) left, and 10 animals (20.8%) disappeared, died, or could not be located. Similarly in connected patches, 10 cotton rats (20.0%) stayed, 29 (60.0%) left, and 9 (18.8%) were unaccounted. There was no significant difference within treatments regarding the gender of animals leaving connected patches ($X^2 = 1.04$, $df = 1$, $P = 0.31$) or isolated patches ($X^2 = 0.06$, $df = 1$, $P = 0.81$). The shape of the curves showing the proportion of individuals remaining in the release patch over time for each treatment did not significantly differ (Wilcoxon $X^2 = 0.31$, $P = 0.58$; Figure 2). The curves in Figure 2 incorporate the data on missing animals. As such, the proportions remaining in the patch of release at the end of the study period are slightly higher than the proportions given above. Likewise, there was no significant difference in gender regarding the proportion of individuals remaining in a patch over time (Wilcoxon $X^2 = 2.08$, $P = 0.15$). On average, 2.7 days (± 0.27 SE) were spent in a patch before moving to another patch.

Cotton rats used corridors in several ways. In connected patches, 7 cotton rats (24%) used a corridor to leave the patch, whereas 22 cotton rats (76%) left through the forest. The expected percentage of animals leaving a patch via the corridor was 6%. Therefore, selection for the corridor as an exit route was significant ($Z = 3.99$, $P < 0.01$). Animals that exited via a corridor did so on average 2.4 days following release. Of the 7 cotton rats that left the release patch through a corridor, 4 animals colonized another patch via the corridor, 2 remained in the corridor, and 1 individual returned to the patch of release.

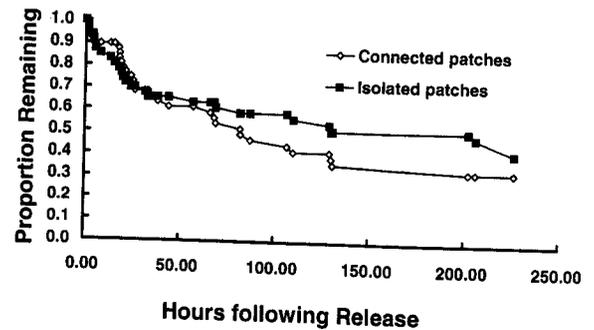


Figure 2. Proportion of cotton rats remaining in patch of release over the course of the study per treatment type. Proportions did not differ significantly ($P > 0.05$) between connected and isolated patches.

Success of colonization

Colonization was defined as when a cotton rat was located in a patch other than its patch of release. Colonization does not imply establishment of a home range or breeding success. Of the 53 cotton rats that left their release patch, 23 (43%) colonized another patch. Cotton rats leaving both isolated and connected patches were equally successful at colonizing another patch as expected based on the availability of receptor patches (isolated: $X^2 = 5.76$, $df = 3$, $P = 0.12$; connected: $X^2 = 9.96$, $df = 5$, $P = 0.08$).

Of the 23 animals that colonized another patch, only 13 (4 from isolated patches, 9 from connected) remained solely in that second patch (Figure 3a,b). The other 10 animals made several ($\bar{x} = 2.8$) interpatch movements (Figure 3c,d). Of the 10 cotton rats that made more than one interpatch journey, 9 returned at least once to their respective patch of release.

In addition to moving through the forest matrix, cotton rats used the forest as habitat (Table 1). Short-term ($\bar{x} = 1.7 \pm 0.5$ SE days) explorations were usually within 30 m of the edge of the patch. Animals remained in the forest matrix for 3.5 (± 1.6 SE) days and moved a mean distance of 186 m (± 154 SE) from the release patch.

Mean net distances moved

The mean net distance moved for animals released into connected patches (226 m \pm 53 SE) and isolated patches (194 m \pm 58 SE) at the end of ten days did not differ significantly ($F = 0.28$, $df = 1,32$, $P = 0.60$). Differences in mean net distance moved by gender also did not differ significantly ($F = 0.19$, $df = 1,32$, $P = 0.66$). Likewise, no significant seasonal differ-

Table 1. Use of the forest matrix by *Sigmodon hispidus* for temporary exploratory behavior or extended occupancy following release from isolated (I) and connected (C) patches.

Treatment	Sex	Total time in forest (days)	Distance from release patch (m)	Behavior
I	Female	1.0	15	Remained in forest.
C	Female	9.0	300	Remained in forest.
C	Female	2.0	760	Remained in forest.
C	Male	5.0	400	Remained in forest.
I	Female	3.0	15	Explored forest matrix but returned to patch of release.
C	Female	0.3	15	Explored forest matrix but returned to patch of release.
C	Female	0.5	15	Explored forest matrix but returned to patch of release.
I	Female	0.3	20	Explored forest matrix but returned to patch of release.
C	Female	2.0	30	Explored forest matrix but returned to patch of release.
C	Male	1.0	15	Explored forest matrix but returned to patch of release.
C	Female	1.1	5	Explored forest matrix but returned to patch of release.
C	Male	3.0	15	Explored forest matrix but returned to patch of release.

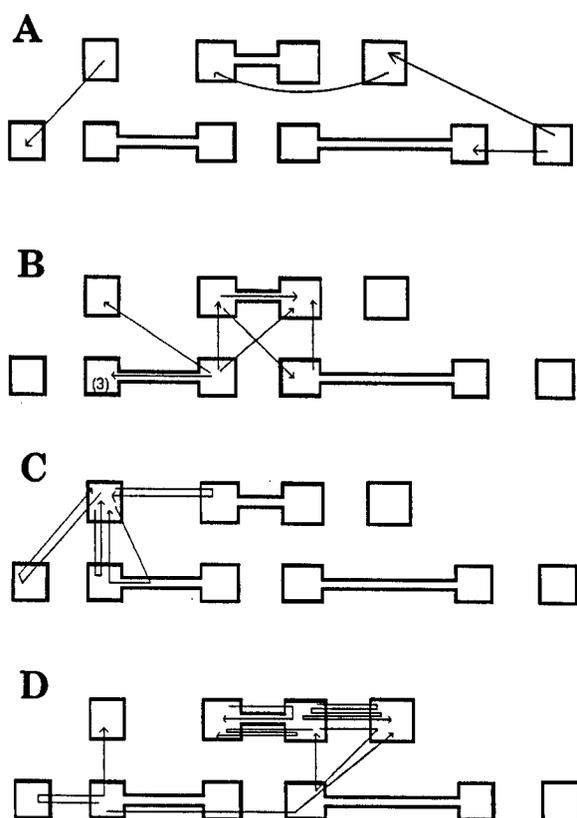


Figure 3. Movement of cotton rats between experimental patches. Cotton rats making a single interpatch movement from isolated patches of release (A) and from connected patches of release (B). Multiple interpatch movements were made by cotton rats leaving both isolated patches of release (C) and leaving connected patches of release (D). Each arrow represents the movement of one animal, except where noted by a movement value in parenthesis.

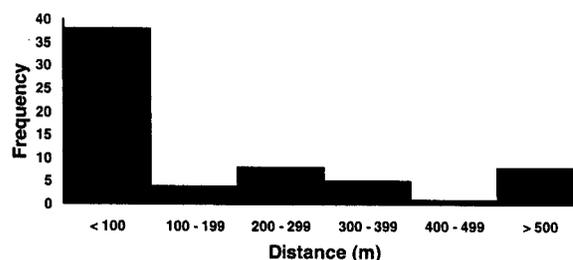


Figure 4. Frequency histogram depicting net distance moved by cotton rats at the conclusion of the 10-day period of release.

ences as related to distances moved by cotton rats were detected ($F = 0.26$, $df = 3,4$, $P = 0.85$).

Most animals ($n = 38$) moved a net distance of less than 100 m (Figure 4). Thirteen animals (6 males, 7 females) made long-distance movements out of the study area ($\bar{x} = 708$ m; range = 249–1435 m), and traversed a variety of habitat types. In addition to the 13 animals that left the study site, seven cotton rats (5 females, 2 males) moved greater than 300 m within the study area to colonize a different patch or corridor ($\bar{x} = 511$ m, range = 344–937 m).

Daily patterns of activity

A significant difference ($F = 4.88$, $df = 5,300$, $P < 0.01$, Greenhouse–Geisser value = .001) was found regarding the distance moved by cotton rats during specific periods of time. This difference was attributed to a significant interaction ($F = 3.13$, $df = 5,300$, $P < 0.01$, Greenhouse–Geisser value = 0.017)

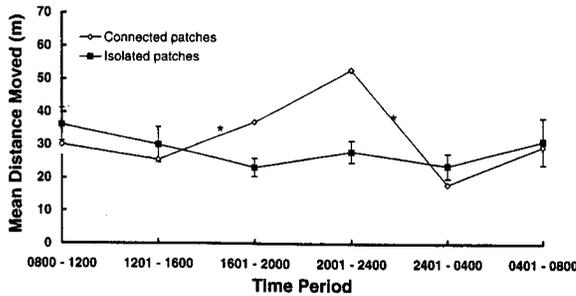


Figure 5. Mean distances (\pm SE) moved by cotton rats per time period. Asterisks indicate a significant difference ($P < 0.05$) in the slope between treatments.

between treatment type and distance moved. Mean distances moved by animals released into isolated treatments were significantly less than mean values for individuals released in connected treatments at 1601–2000 h ($F = 4.81$, $df = 1,60$, $P < 0.05$) and 2001–2400 h ($F = 6.06$, $df = 1,60$, $P < 0.05$; Figure 5).

Direction of movement

Final location of individual cotton rats were uniformly distributed for both the connected ($z = 0.76$, $P > 0.05$) and isolated ($z = 1.01$, $P > 0.05$) treatments. Animals that left the patch were uniformly distributed for both connected ($z = 0.66$, $P > 0.05$) and isolated ($z = 0.18$, $P > 0.05$) treatments. The final location of cotton rats that left the patches, regardless of treatment, were uniformly distributed ($z = 0.67$, $P > 0.05$).

Selection of vegetation by cotton rats

Cotton rats significantly selected percent cover of vegetation differently from that which was available in patches and corridors ($F = 4.22$, $df = 1,98$, $P < 0.05$). Mean total vegetative cover at specific sites where cotton rats were located was 28.8% (± 0.9 SE), whereas the mean value was 26.0% (± 1.1 SE) for vegetative cover at random sites. Cotton rats did not select for percent cover of any particular vegetation type (i.e., shrubs, vines, grasses, forbs; $F = 1.38$, $df = 3, 3614$, $P = 0.25$) in patches and corridors. The mean percent cover for forbs was 17.6 (± 1.3 SE), for grasses was 22.9 (± 1.4 SE), for shrubs was 38.9 (± 1.7 SE), and for vines was 30.1 (± 1.89 SE). However, selection did occur regarding shrub height ($F = 12.15$, $df = 3,3611$, $P < 0.001$). A significant interaction between percent cover and shrub height also existed ($F = 4.32$,

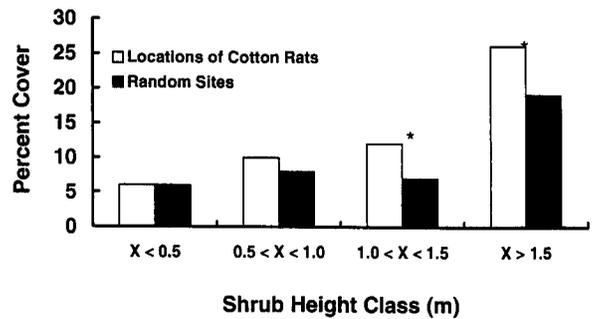


Figure 6. Selection by cotton rats for shrub height in patches/corridors compared to mean available vegetation found in patches/corridors. Asterisks indicate a significant difference ($P < 0.05$) between shrub height in which cotton rats were located and shrub height at random sites within patches/corridors.

$df = 3,3611$, $P < 0.01$). Cotton rats preferred sites with tall (> 1 m) shrubs and with high percent cover (Figure 6). In contrast, selection was not found for herbaceous (grass and forb) height ($F = 0.14$, $df = 1, 98$, $P = 0.71$). No strong correlation existed between any vegetation types.

In the forest matrix, cotton rats did not significantly select vegetative cover differently from that available ($F = 3.00$, $df = 1,111$, $P = 0.09$). However, cotton rats did select for sites with a high percent cover of vines and low tree canopy cover ($F = 9.33$, $df = 5, 1201$, $P < 0.001$; Figure 7). An analysis of plant height revealed a preference by cotton rats for herbaceous vegetation ($F = 4.61$, $df = 1,111$, $P < 0.05$), but not for a particular herbaceous height ($F = 1.31$, $df = 2, 576$, $P = 0.27$). Selection did not occur for either percent cover of shrubs ($F = 0.17$, $df = 1, 111$, $P = 0.68$), shrub height ($F = 1.73$, $df = 3, 805$, $P = 0.16$), or woody debris ($F = 3.29$, $df = 1, 109$, $P = 0.07$) in the forest matrix. A strong positive correlation existed between grasses and forbs (covariance = 0.50). A strong negative correlation existed between canopy cover and cover of forbs (covariance = -0.49), canopy cover and cover of grasses (covariance = -0.73), and vine cover and cover of grasses (covariance = -0.31).

Discussion

Results supported the hypothesis that the forest matrix would not inhibit movements of cotton rats. For example, 50% of the released animals entered and moved through the matrix. These findings are not without precedent. For example, Briese and Smith

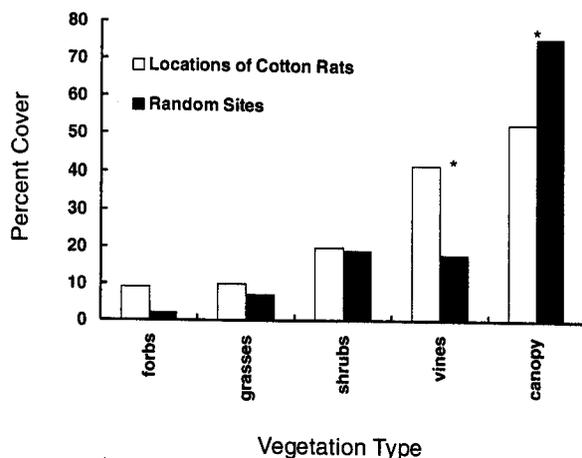


Figure 7. Selection by cotton rats for specific vegetation types in the forest matrix compared to mean available vegetation in the forest matrix. Asterisks indicate a significant difference ($P < 0.05$) between vegetation types in which cotton rats were located and vegetation types at random sites within the forest matrix.

(1974) found that 13% of cotton rat captures in a study on the Savannah River Site (SRS) occurred in wooded habitats. These animals were thought to be innate dispersers moving through unfavorable habitat. Golley et al. (1965), in a study also on the SRS, captured cotton rats in hardwood forests but not in pine forests. Layne (1974), however, documented resident populations of cotton rats in pine flatwoods in northern Florida.

We also tested the prediction that corridors do not affect patterns of movement. This prediction had two components: (1) the number of cotton rats leaving connected and isolated patches will not significantly differ and (2) the number cotton rats leaving a connected patch will not prefer corridors over the forest matrix as a route of exit. The first component of the prediction was supported by the observations that statistically equal numbers of cotton rats (total and for each sex) left isolated and connected patches. This finding is in contrast with other investigations. LaPolla and Barrett (1993), for example, found that more male meadow voles (*Microtus pennsylvanicus*) dispersed from connected patches than from patches without a corridor.

Cotton rats demonstrated a clear preference to leave connected patches through the corridor rather than through the forest matrix. This finding regarding corridor use by small mammals is supported by several other investigations (Bennett 1990; Lorenz and Barrett 1990; Merriam and Lanoue 1990; LaPolla and Barrett 1993). Preference for leaving a patch via a cor-

ridor is essential in determining the need for corridors. However, one also needs to know if that preference translates into greater colonization success.

Failure to reject the null hypothesis that the forest matrix inhibited movements by cotton rats led to the prediction that animals leaving isolated and connected patches would be equally successful in colonizing another patch (i.e., cotton rats leaving isolated and connected patches were as successful as expected in finding another patch). Even though corridors were the preferred route to leave a patch, corridor use did not translate into greater overall colonization success. An explanation of this finding requires an examination of the purpose of a corridor. A corridor is intended to facilitate movement from one habitat to another (Lidicker and Koenig 1996). Rosenberg et al. (1997) noted, however, that corridors may function as an extension of patch habitat rather than to facilitate movement between patches of habitat. The facilitation of movement should result in an increase in connectivity (i.e., the probability that an organism will move from patch 'A' to patch 'B'; Merriam 1995). However, if connectivity between and among habitat patches is already high, then corridors will not be necessary. In this landscape, the forest matrix appeared to provide adequate connectivity among patches.

Corridors could also affect colonization of patches by influencing the direction in which an animal settled. Corridors were oriented east to west in this landscape. Corridors could, therefore, theoretically direct movement in either an eastward or westward direction. However, the final locations of individual cotton rats that left patches of release were evenly distributed regardless of treatment. Thus, corridors had no significant affect regarding where cotton rats settled.

Results supported the hypothesis that the net distance moved by cotton rats would not differ between treatments. Since the matrix did not inhibit cotton rat movement and corridors do not promote colonization, these findings were not surprising. Although significant corridor use by cotton rats did exist, movements were not limited to the corridor. As such, net distance moved did not differ between treatments. Unfortunately, our results cannot be directly compared to other experimental studies of corridor use because of the small-scale of other experiments.

Our findings of long-distance movements by cotton rats are supported by previous observations regarding long-distance movements by small mammals. Goertz (1964) reported cotton rat movements of up to 400 m. Displaced dusky-footed woodrats (*Neotoma*

fuscipes) were found to move an average of 885 m (Smith 1965). Merriam and Lanoue (1990) observed that white-footed mice (*Peromyscus leucopus*) translocated from forest and cropland habitats traveled an average of 135 and 168 m, respectively, in two days and resident animals moved 156 m in two days. Szaeki and Liro (1991) found that over 50% of field mice (*Apodemus agrarius*) and bank voles (*Clethrionomus glareolus*) moved greater than 300 m in heterogeneous environments. Kozakiewicz et al. (1993) similarly found that bank voles moved an average of 243 m heterogeneous habitats.

The evidence for long-distance travel by cotton rats is especially interesting because not only did these animals move great distances, but they crossed many habitat types in the process. Neither age-class nor type of forest habitat appeared to hinder movements by cotton rats. As discussed earlier, since cotton rats have been observed in forested habitats, this result was not particularly surprising. However, landscape features that would appear to be a barrier to movement failed to prevent such movement. For example, several cotton rats crossed a four-lane paved road. Swihart and Slade (1984) demonstrated that roads were barriers to movements within cotton rat home ranges. The inhibitory effects of roads to movements have also been shown for white-footed mice and bank voles (Kozakiewicz 1993). Perhaps the effect of roads on movements depends on the behavioral state of the animal. For example, individuals may be more sensitive to barriers during home range movements, but less sensitive to barriers during dispersal or exploratory excursions. Wetlands and streams also did not block cotton rat movements. This supports Esher et al. (1978) claim that narrow bodies of water were not a barrier to cotton rat movements. The lack of clear barriers to cotton rat movements suggests that they should be able to reach and colonize a diversity of habitat-types regardless of apparent isolation. This mobility could decrease the probability of localized extinction (Fahrig and Merriam 1994). However, an important caveat must be recognized. This study showed that individual cotton rats are capable of moving over apparent barriers, but it does not address the critical subject of how frequently such movements occur. Although an occasional cotton rat may cross a road, many more cotton rats may be inhibited. Thus, a road does not prevent absolute movement, but it may affect the frequency of movement. The present study did not address this important distinction.

The finding that net distance moved did not differ between sexes was somewhat surprising. A large body of literature supports the claim that male small mammals move greater distances than females (Greenwood 1980, and references cited therein; Wolff 1993). Dispersal in small mammals has also been found to be male biased (Greenwood 1980), whereas females tend to be more territorial and sedentary (Lambin 1994). However, Goertz (1964) documented that both male and female cotton rats make long-distance movements. Thus, the extent and gender bias of movement may differ depending on the type of movement observed. In this study, the animals were translocated. As such, they did not have established home ranges in the experimental patches. Thus, there likely was greater propensity to explore than to settle in the patch of release. The observed movements from the patch of release to another patch and then return to the original patch demonstrates the spatial extent to which cotton rats can explore in a short amount of time. These explorations were likely an attempt to establish a home range.

Interestingly, daily patterns of activity differed between treatments. Activity increased in the connected patches from 1600 to 2400 h with a peak between 2001 and 2400 h. Activity within the isolated patches remained relatively constant. Cameron et al. (1979) found cotton rats to be active all day with peaks at 1900 and 0900 h and troughs between 2300 and 0500 h. Our results for individuals in the connected treatment were in agreement with the crepuscular behavior of cotton rats. However, it is unclear why a disparity existed between treatments.

The fourth prediction was that movements would be associated with particular vegetation characteristics at the microhabitat scale. Our findings indicated that this prediction was correct in both patch/corridor and matrix habitats. However, the vegetation associations differed in these contrasting habitat types. Vegetation characteristics at the microhabitat scale affected where cotton rats were located. For example, cotton rats were found within patches and corridors at locations with a high percent cover of vegetation. Numerous studies have also demonstrated a preference by cotton rats for dense cover (Goertz 1964; Golley et al. 1965; Kincaid et al. 1983; Spencer and Cameron 1983; Lidicker et al. 1992). Spencer and Cameron (1983) observed that individuals inhabiting patches containing shrubs were larger, more frequently in reproductive condition, and moved greater distances. This supports our finding that

cotton rats preferred areas with tall shrubs and a high degree of cover.

Vegetation use by cotton rats in the forest matrix differed from usage in patch and corridor habitats. This suggests that cotton rats can detect or have different selection preferences while in transit. Vines supplied excellent ground cover but were negatively correlated with herbaceous growth, the latter being the preferred diet of cotton rats (Kincaid and Cameron 1985). However, cotton rats were often found in open-canopy areas containing herbaceous vegetation. Transients would benefit from a juxtaposition of cover and food supply by having adequate resources for survival at one location. Because risk of predation is higher for animals in transit (Metsgar 1967; Ambrose 1972), an animal would not be expected to forage far from cover. Cotton rats in this study selected sites having high percent cover of vines and low tree canopy cover which provided both food and cover.

Results of our investigation demonstrated that cotton rats are able to move through the landscape using all elements of that landscape (patches, corridors, and matrix). In fact, movements by cotton rats appear to have few spatial limitations. The evidence of long-distance movements by cotton rats further supports the hypothesis that small mammals are capable of moving greater distances than commonly believed (Crawley 1969; Furrer 1973; Clark et al. 1988; Szacki and Liro 1991; Kozakiewicz et al. 1993; Szacki et al. 1993). This mobility was facilitated by microhabitat characteristics of landscape elements. Differential vegetation utilization by cotton rats among patch/corridor and matrix habitat suggests that cotton rats have greater behavioral plasticity than previously reported. A dispersing animal may select vegetation differently than an animal moving within a home range. Future research addressing the role of landscape structures on the movements of small mammals should consider both micro- and macrohabitat components and variations.

The observed abilities of cotton rats to move long distances and traverse different habitat types could have important implications to metapopulation theory (Levins 1970). If the long-distance movements observed in this study are common, then the spatial activity of cotton rats would allow such a high degree of interaction between individuals that subpopulations are not established in single habitat patches. This situation violates Levin's (1970) original model but would satisfy Harrison's (1991) 'patchy population' modification of the metapopulation model. However, more

information on the frequency of long-distance movements by resident animals is needed before a definitive answer is reached.

The use of landscape patches and corridors by small mammal species appears to be influenced by the ecology and behavior of that species and on the characteristics of the surrounding matrix (i.e., use of landscape elements and movement behavior by small mammals appear to be species specific). The cotton rat, for example, uses all landscape elements during its movements. A species may show a preference for a corridor but that preference is inconsequential if enough movement occurs through the matrix, as was the case for the cotton rats in this study. To address the effects of habitat fragmentation, ecologists need to better understand to which attributes of the corridor and matrix a particular animal is actually responding. By understanding species-specific responses to micro- and macrohabitat characteristics of landscape elements, natural resource managers should be able to increase connectivity between patches by enhancing the spatially-dominant matrix. In certain situations, a conservation strategy that focuses on improving connectivity by altering characteristics of the matrix, for example, may be more ecologically effective and economically feasible for a diversity of animal species than by focusing on landscape corridors. Individual animals, for example, may be perceiving corridors within the matrix. Indeed, Gustafson and Gardner (1996) demonstrated that corridors can be diffuse and difficult to identify. If connectivity is a threshold phenomenon (With et al. 1997), the goal of conservation should be to maintain landscape connectivity above a minimum threshold. Whether that degree of connectivity is best achieved through management of the matrix or establishment of a corridor will likely depend on the characteristics of the matrix and of the behavioral ecology of a particular species in question. A greater emphasis on the behavioral basis of observed movement at the landscape level is needed before such issues can be resolved (Lima and Zollner 1996). The role of matrix or corridor habitats (Rosenberg et al. 1997) in providing connectivity will depend on if and how an animal responds to these landscape elements. Cotton rats, for example, appear to find characteristics within a pine forest matrix and in human-established corridors as suitable for movement.

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