KAREN ELIZABETH MABRY
Effects of Landscape Elements on Population Densities, Habitat Utilization, Home Ranges, and Movements of Three Small Mammal Species
(Under the Direction of GARY W. BARRETT)

The effects of landscape fragmentation on plant and animal populations have become more important with increasing human influence on landscapes, however, little research has focused on use of the entire landscape, including patch, corridor, and matrix habitats. This study addresses the effects of corridors and habitat enrichment in an experimentally fragmented landscape on population densities, home range sizes, and movement patterns of the cotton rat (*Sigmodon hispidus*), cotton mouse (*Peromyscus gossypinus*), and old-field mouse (*P. polionotus*). Small mammal populations were monitored by live-trapping and radio-telemetry. Neither corridors nor habitat enrichment had a significant effect on population densities or home range sizes of any species. Relative use of patch interiors, edges, and corridors was assessed. Cotton rats were trapped within corridors more often than expected, while cotton mice and old-field mice were trapped within patch interiors more often. Cotton mice and old-field mice were more likely to emigrate from connected than isolated patches.

INDEX WORDS: Corridor, Fragmentation, Home range, Movement, *Peromyscus gossypinus*, *Peromyscus polionotus*, *Sigmodon hispidus*

EFFECTS OF LANDSCAPE ELEMENTS ON POPULATION DENSITIES, HABITAT UTILIZATION, HOME RANGES, AND MOVEMENTS OF THREE SMALL MAMMAL SPECIES

by

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B.S. Clemson University, 1999

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial
Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2001

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ACKNOWLEDGEMENTS

I thank my major professor, Gary W. Barrett, for his help and guidance during my master's program at the University of Georgia. I would also like to thank my other committee members; Mike Smith, my faculty sponsor at SREL, was always available when I had questions and concerns, Sara Schweitzer stepped in at the last minute with excellent suggestions, and Frank Golley offered advice and encouragement.

Many individuals helped gather the data presented here; John Peles, David Bowne, and Erin Dreelin have all led this project over the years. Kristin Biris, Carrie Brooks, Cory Christopher, Josh Jamell, Audrey Majeske, Alison Pruett, and especially Lindy Paddock worked on the corridor project for at least 1 field season. Cacye Payton conducted library work.

I am especially grateful to those who volunteered to help in the field; they gave up weekends to get up at first light to check traps and stomp through the woods in the dark laden with telemetry equipment – all without financial compensation! Cory Christopher, Emily Cox, Chris Kittle, Ryan Klee, Nate Nazdrowicz, Natalie Powell, Alison Pruett, and Arlena Wartell all volunteered to help in the field.

Paul Johns of SREL helped with many practical issues and allowed me to use his traps. The SREL computer lab staff and Deno Karapatakis of the SREL GIS lab helped with technical aspects, such as keeping my home range analysis program running and working with aerial photos and GIS.

I also had help with data analysis; Julie Weston taught me to use Calhome and gave great advice about telemetry and home range analysis. Jeanne Epstein in the Institute of Ecology GIS lab taught me everything I needed to know about using ArcView. I consulted Dan Hall and Steve Rathbun in the Statistics Department about analysis, and Lihua Wang of Statistical Consulting ran the generalized estimating equation analysis.

I thank Nick Haddad and Robert Cheney for allowing us to use the fragmented landscape they designed; I never would have been able to conduct a master’s project on such a scale without their help!

I am also indebted to the USDA Savannah River Forest Station, particularly John Blake and John Kilgo, who have supported this project over the years. Most of the funding for this project came from the Forest Service (grant numbers 10-21-RR551-125 and 10-21-RR551-144); the Forest Service also maintained the landscape patches, provided us with a vehicle and radios, and other logistical support. Ed Olson answered all my questions about practical issues.

This project was conducted under Cooperative Agreement DE-FC09-96SR 18546 between the United States Department of Energy and the University of Georgia Research Foundation. I was supported by a National Science Foundation Graduate Research Fellowship during this study.

Finally, I thank my family and friends for their support, even if they’re a little confused about why I’ve devoted 2 years of my life to studying mice. Many friends have helped me keep everything in perspective, especially Emily Cox and Cory Christopher.

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INTRODUCTION AND LITERATURE REVIEW

Increasing human influence has caused landscapes to become more fragmented, and the impact of fragmented landscapes on plant and animal populations has become an important issue in conservation biology. Landscape mosaics are composed of habitat patches, connecting corridors, and an intervening matrix of less-suitable habitat (Forman and Godron 1981). Spatial heterogeneity influences ecological systems in many ways (Robinson et al. 1992; Wiens et al. 1993). For example, the ability of a fragmented landscape to support a population is influenced by the proportion of suitable habitat (Andrén 1994); size, shape, and quality of habitat patches (Kozakiewicz 1993); ability of the organism to move between and among habitat patches, which can be influenced by the presence and characteristicsof corridors (Fahrig and Merriam 1985, 1994; Szacki and Liro 1991; La Polla and Barrett 1993; Anderson and Danielson 1997; Krohne 1997; McIntyre and Hobbs 1999); distance to the nearest source population (MacArthur and Wilson 1967); and behavioral responses to fragmentation (Yahner and Mahan 1997). Modeling studies predict that population densities will be higher in patches connected by corridors (e.g., Henein and Merriam 1990), and observational studies frequently document the presence of animals in corridors (e.g., Downes et al. 1997). Yet there is little experimental evidence that corridors actually increase population densities (Beier and Noss 1998), and few investigators have considered the influence of the landscape matrix on populations in fragmented landscapes (but see Ricketts 2001).

More subtle variation, such as differences in habitat quality, in heterogeneous landscapes may also affect population dynamics of small mammals. Experimental habitat enrichment has a positive effect on population densities of hispid cotton rats (*Sigmodon* *hispidus*) (Doonan and Slade 1995; Eshelman and Cameron 1996) and meadow voles (*Microtus pennsylvanicus*) (Desy and Batzli 1989; Peles and Barrett 1996). Lin and Batzli (2001) found that increased cover resulted in higher habitat quality for prairie voles (*M. ochrogaster*). Nutrient inputs increase primary productivity (Carson and Barrett 1988; Polis et al. 1997) and food resources, and herbivorous mammals have been found to forage more frequently in fertilized than control plots (Ball et al. 2000).

Few studies have compared the relative use of landscape elements by small mammals; however, Lidicker and Peterson (1999) found that gray-tailed voles (*M. canicaudus*) were captured significantly more often in traps located in the interior rather than the edge of habitat patches. Lidicker (1999) suggested that edge effects were highly species-specific; some small mammal species benefit from habitat edges, while others avoid edges. As corridors typically have a high proportion of edge habitat, the response of a species to edge habitat is important in determining whether a corridor will be effective. For example, a long narrow corridor is not likely to be used by a species that avoids edge habitat.

Of the 4 fundamental processes affecting population dynamics (birth, death, immigration and emigration), immigration and emigration are the most difficult to measure and have frequently been ignored by ecologists (Turchin 1998). Inclusion of corridors to increase movement through fragmented landscapes has become common in conservation and land management plans (Rosenberg et al. 1997); however, neither the actual use of corridors nor movement through the "hostile" matrix surrounding suitable habitat patches is commonly quantified (Beier and Noss 1998). Connectivity is meaningful only in the context of a particular species inhabiting a particular landscape; Tischendorf and Fahrig (2000) make an important distinction between corridors and connectivity. The presence of a corridor in a landscape does not necessarily mean that the landscape has high connectivity, nor does the absence of a corridor mean that it is not highly connected. A fragmented landscape with no corridors between patches may be highly connected if the species in question is capable of moving through the matrix habitat between patches, and connectivity may vary with species

(McIntyre and Hobbs 1999). The assumption that corridors increase interpatch movement rates remains largely untested, and the effects of matrix habitat, frequently assumed to be "inhospitable," on movement behavior remain unclear.

This long-term investigation was designed to evaluate the effects of patch connectivity and habitat quality on the population dynamics, habitat utilization, home range size, and movements of 3 small mammal species, the cotton rat, a generalist rodent frequently found in old-fields; the cotton mouse (*Peromyscus gossypinus*), a habitat generalist found in many different habitat types; and the old-field mouse (*P. polionotus*), which prefers open, sandy habitats (Golley et al. 1965). We tested the response of small mammal populations to patch connectivity and habitat enrichment by manipulating these factors in an experimentally fragmented 110-ha landscape (see Haddad 1999). The hypotheses tested were: small mammal population densities will be higher in connected rather than isolated patches of equal size, small mammal population densities will be higher in enriched rather than non-enriched patches, cotton mice will use all habitat types (patch edge, patch interior, corridor) equally while cotton rats and old-field mice will preferentially use interior habitats, and increased movement should lead to larger home range sizes in connected rather than in isolated patches. As cotton mice are considered habitat generalists, while the other 2 species are more restricted to open areas, such as the clear-cuts used in this study (Golley 1965; Danielson and Anderson 1999), we predicted that cotton mice would move more frequently among patches that were not connected to each other than would the other 2 species. Such investigations are essential to provide information on the effects of habitat fragmentation on natural populations.

This thesis is composed of 2 chapters. The first addresses the effects of landscape elements on population dynamics of small mammals and will be revised and submitted to the Journal of Mammalogy as authored by K.E. Mabry, E.A. Dreelin, and G.W. Barrett. The second addresses the role of landscape elements on movement patterns and will be revised and submitted to Landscape Ecology as authored by K.E. Mabry and G.W. Barrett.

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CHAPTER 1

INFLUENCE OF LANDSCAPE ELEMENTS AND HABITAT ENRICHMENT ON POPULATION DENSITIES AND HABITAT SELECTION OF THREE SMALL MAMMAL SPECIES

ABSTRACT

The effects of patch connectivity and habitat enrichment on population densities and habitat utilization of 3 small mammal species on the Savannah River Site (SRS) in Aiken County, South Carolina were assessed during a long-term (1997-2000) study in an experimentally fragmented landscape. No significant differences were found in the population densities of any species in connected vs. isolated or enriched vs. non-enriched habitat patches. However, trends in population densities indicate that connected patches usually supported higher densities of cotton rats (*Sigmodon hispidus*), and isolated patches supported higher densities of old-field mice (*Peromyscus polionotus*). No significant trends in population densities were observed for cotton mice (*P. gossypinus*). Cotton rats were captured more often in corridors than in either the interior or edge of habitat patches, while old-field mice were captured more frequently in the interior. Cotton mice exhibited a more uniform distribution across habitat types; however, during 1999 and 2000 cotton mice were trapped more frequently than expected in interior traps. Two cotton mice were trapped within the forest matrix on 5 occasions; cotton rats and old-field mice were never trapped within the forest matrix. Home ranges of individual cotton mice frequently included 2 habitat patches and the intervening matrix. The mean proportion of cotton mouse home ranges in patch rather than matrix habitat ranged from 1.6 to 80.2 % (mean = 39.9%). These results suggest that landscape fragmentation may have less of an effect on cotton mice, a habitat generalist.

Key words: *corridor, fragmentation, habitat selection, habitat quality, matrix, patch, Peromyscus gossypinus, Peromyscus polionotus, Sigmodon hispidus*

INTRODUCTION

Landscape mosaics are composed of patches of suitable habitat, connecting corridors, and an intervening matrix of less-suitable habitat (Forman and Godron 1981). Spatial heterogeneity influences ecological systems in many ways (Robinson et al. 1992; Wiens et al. 1993). For example, the ability of a fragmented landscape to support a population is influenced by the proportion of suitable habitat (Andrén 1994); size, shape, and quality of habitat patches (Kozakiewicz 1993); ability of the organism to move between and among habitat patches, which can be influenced by the presence of corridors (Fahrig and Merriam 1985, 1994; Szacki and Liro 1991; La Polla and Barrett 1993; Anderson and Danielson 1997; Krohne 1997; McIntyre and Hobbs 1999); distance to the nearest source population (MacArthur and Wilson 1967); and behavioral responses to fragmentation (Yahner and Mahan 1997). This long-term study was designed to test the effects of patch connectivity and habitat quality on the population dynamics of 3 small mammal species, the cotton rat (*Sigmodon hispidus*), a generalist rodent frequently found in old-fields; the cotton mouse (*Peromyscus gossypinus*), a habitat generalist found in many different habitat types; and the old-field mouse (*P. polionotus*), which prefers open, sandy habitats (Golley et al. 1965).

There are few general principles for predicting the response of small mammal populations to habitat fragmentation. A review of fragmentation studies on multiple taxa found that species abundance or population density decreased with fragmentation in 6 of 13 experimental studies, but that small mammal populations tended to show increasing densities with fragmentation (Debinski and Holt 2000). Although much insight into the effects of fragmentation on population dynamics of small mammals has been gained through both experimental and observational studies (Diffendorfer et al. 1995; Collins and Barrett 1997; Barrett and Peles 1999a,b); the effects of fragmentation on the abundance and distribution of vertebrates are unpredictable and further investigation is warranted.

Fragmentation of formerly intact habitat often results in a metapopulation structure, a "population of populations" inhabiting remnant habitat patches that are connected by infrequent movement of individuals (Hanski 1999). Metapopulation dynamics are influenced by the presence, number, and quality of corridors between and among habitat patches (Fahrig and Merriam 1985; Henein and Merriam 1990; Anderson and Danielson 1997). Connected patches are predicted to have higher population densities than isolated patches because connecting corridors should increase available habitat (Rosenberg et al. 1997); increase movement between patches, thus increasing colonization rates of unoccupied patches (Brown and Kodric-Brown 1977; Lorenz and Barrett 1990; Hanksi and Gilpin 1991; La Polla and Barrett 1993, Rosenberg et al. 1997); increase gene flow (Aars and Ims 1999); and decrease variability in birth and death rates (Beier 1993). Modeling studies predict that population densities will be higher in patches connected by corridors (e.g., Henein and Merriam 1990), and observational studies frequently document the presence of animals in corridors (e.g., Downes et al. 1997), yet there is little experimental evidence that corridors actually increase population densities (Beier and Noss 1998). However, the presence of corridors in experimental landscapes positively influenced population densities of certain butterflies (Haddad and Baum 1999) and of meadow voles (*Microtus pennsylvanicus*) (La Polla and Barrett 1993).

Response of animal species to corridors is highly variable; for example, corridors are more effective for species that exhibit increased turning behavior at habitat edges (Haddad 1999). While matrix habitat is not necessarily a total barrier to movement (Bowne et al. 1999), it is typically less conducive to movement than patch habitat, and the ability to move through matrix habitat varies with species, matrix habitat type, and edge "hardness" (Stamps et al. 1987; Kozakiewicz 1993; McIntyre and Hobbs 1999; Ricketts 2001). Habitat generalists may be less affected by habitat fragmentation than are habitat specialists; Mech and Hallett (2001) report that *P. maniculatus* populations inhabiting connected and isolated patches have similar genetic distances, while the presence of corridors does seem to decrease genetic distance for the red-backed vole (*Clethrionomys gapperi*), a habitat specialist. Mossman and Waser (2001) report that habitat fragmentation has few effects on *P. leucopus* genetic structure, suggesting that movement between patches may be fairly common, even without corridors. The positive effects of corridors may be offset by problems such as increased transmittal of disease and increased predation (Simberloff and Cox 1987; Hobbs 1992; Harrison and Bruna 1999).

The relationship between population density and habitat quality is well established; experimental habitat enrichment had a positive effect on population densities of hispid cotton rats (Doonan and Slade 1995; Eshelman and Cameron 1996), and meadow voles (Desy and Batzli 1989; Peles and Barrett 1996). Doonan and Slade (1995) found that experimentally increasing the quantity of food led to increased reproduction and immigration into supplemented patches. Lin and Batzli (2001) found that higher cover led to increased habitat quality for prairie voles (*M. ochrogaster*). Nutrient inputs generally increase primary productivity (Carson and Barrett 1988; Polis et al. 1997) and food resources, and herbivorous mammals forage more frequently in fertilized than control plots (Ball et al. 2000).

The 3 small mammal species considered in this study vary in their degree of habitat specialization; cotton mice are the most general and old-field mice are the most specialized. Cotton rats are most often found in habitat with a high percentage of herbaceous cover, particularly grasses and vines (Goertz 1964; Cameron and Spencer 1981; Lidicker et al. 1992; Kaufman et al. 2000). Cotton mice are most plentiful in hardwood forests (Golley et al. 1965), however, they are found in most habitat types, including the old fields used in this study. Coarse woody debris (CWD) and herbaceous vegetation are important resources as both cover and food; cotton mice use CWD as movement pathways and sources of invertebrates (Wolfe and Linzey 1977; Loeb 1999; McCay 2000). Old-field mice are found in relatively open, sandy habitats with herbaceous vegetation (Gentry 1966), such as the clear-cuts used in this study.

The density, diversity, and abundance of animals in a fragmented landscape can be affected dramatically by patch size and geometry, including the proportion of edge habitat ("edge effects") (Harper et al. 1993; Nupp and Swihart 1996; Lidicker 1999). Patch size affects density, and both positive and negative relationships between population density and habitat patch size have been observed for a range of small mammal species (Bowers and Matter 1997; Matter 2000). Different authors have also observed different density-area relationships for the same species. For example, Dooley and Bowers (1998) found that population densities of the meadow vole (*M. pennsylvanicus*) were higher in a fragmented landscape with 72% less available habitat than the non-fragmented landscape to which it was compared. Collins and Barrett (1997) found that densities of female meadow voles were significantly higher in fragmented patches compared to intact habitat patches of equal total size for 3 weeks of a 5-month study. Dooley and Bowers (1996) found no density-area relationship for meadow voles.

Both positive (Foster and Gaines 1991) and negative (Smith and Vrieze 1979) density-area relationships have been observed for the cotton rat. A neutral density-area relationship has been observed for the cotton mouse (Smith and Vrieze 1979), however, negative, neutral, and positive relationships have all been observed for the closely related deer mouse (*P. maniculatus*) and the white-footed mouse (*P. leucopus*) (Gottfried 1979; Foster and Gaines 1991; Dooley and Bowers 1996; Nupp and Swihart 1996). The relationship of population densities of old-field mice to habitat patch area has not been addressed. Bender et al. (1998) found that patch size effects were more commonly observed for edge and interior specialists than for habitat generalists, thus patch size effects should be most obvious for the most specialized species, the old-field mouse.

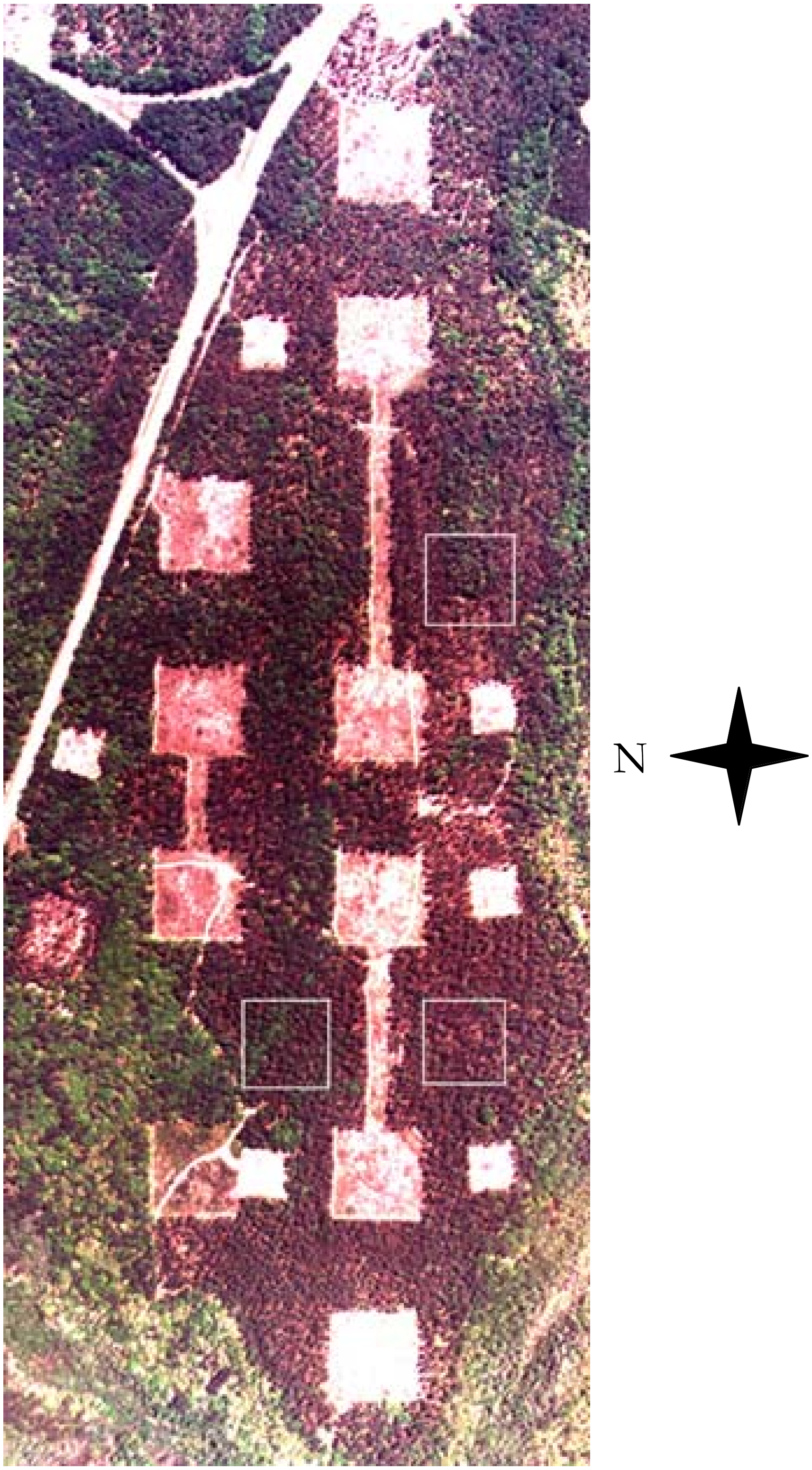
Edge effects influence both biotic and abiotic processes at the transition between two habitat types (Murcia 1995; Lidicker 1999). Lidicker (1999) concluded that edge effects were species-specific; some small mammal species benefit from habitat edges, while others avoid edges. As corridors typically have a high proportion of edge habitat, the response of a species to edge habitat is important in determining whether a corridor will be effective. Few studies have compared the relative use of landscape elements by small mammals; however, Lidicker and Peterson (1999) found that gray-tailed voles (*M. canicaudus*) were captured significantly more often in traps located in the interior of habitat patches than in traps located on the edge of a patch. Increased proportions of edge have been found to have positive effects on the population dynamics of meadow voles (Bowers et al. 1996; Collins and Barrett 1997; Bowers and Dooley 1999).

We tested the response of small mammal population densities to patch connectivity and habitat enrichment by manipulating these factors in an experimentally fragmented 110-ha landscape (Haddad 1999). The hypotheses tested were: small mammal population densities will be higher in connected than in isolated patches of equal size, small mammal population densities will be higher in enriched than in non-enriched patches, and cotton mice will use all habitat types (patch edge, patch interior, corridor) equally while cotton rats and old-field mice will use interior habitats preferentially. Utilization of the pine forest matrix by small mammal species was also assessed; cotton mice were predicted to use the matrix more frequently than either cotton rats or old-field mice.

MATERIALS AND METHODS

Study site.– This study was conducted in an experimentally fragmented landscape on the Savannah River Site (SRS), Aiken County, South Carolina (33°0-25' N, 81°25-50' W). The fragmented landscape consisted of clear-cut patches and corridors embedded within a matrix of managed loblolly pine (*Pinus taeda*) (Fig. 1.1). The experimental landscape consisted of 4 patch types: large (1.6-ha) connected (n=3), large (1.6-ha) isolated (n=3), small (0.4-ha) isolated enriched habitat (n=3), and small (0.4-ha) isolated non-enriched habitat (n=3). Each replicate of the connected treatment consisted of 2 large patches linked by a 32-m wide corridor of length 128, 256, or 384 m. Large patches were established in 1994-1995 by clear cutting and burning (Haddad 1999); small patches were established by the same methods in 1998. All patches were burned and seeded with *Lespedeza cuneata* during winter-spring 1998 to

Figure 1.1. Aerial photograph (1999) of the experimentally fragmented landscape on the Savannah River Site (SRS), Aiken County, South Carolina. Each large patch is 128 x 128 m and each small patch is 64 x 64 m. Locations of forest matrix trapping grids are outlined in white.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return them to a similar stage of old-field secondary succession. Habitat quality was experimentally increased in 3 small patches. During spring 1999 and 2000, these 3 small patches were seeded with *L. cuneata* at a rate of approximately 71 kg/ha and CWD was moved from non-enriched to enriched patches; approximately 12 logs >10 cm diameter at breast height (dbh) were added to each enriched patch. On 9 June 2000, enriched patches were fertilized with 97 kg/ha of fertilizer (19-19-19 N-P-K ratio) to increase primary productivity.

Weather.– The magnitude of the Southeastern drought during 1997-2000 was assessed using data from the National Oceanic and Atmospheric Administration (NOAA 2001). Palmer drought severity indices relate rainfall and temperature in a region to quantify the severity of drought. An index of 0 indicates normal conditions, while increasingly negative indices indicate more severe drought conditions.

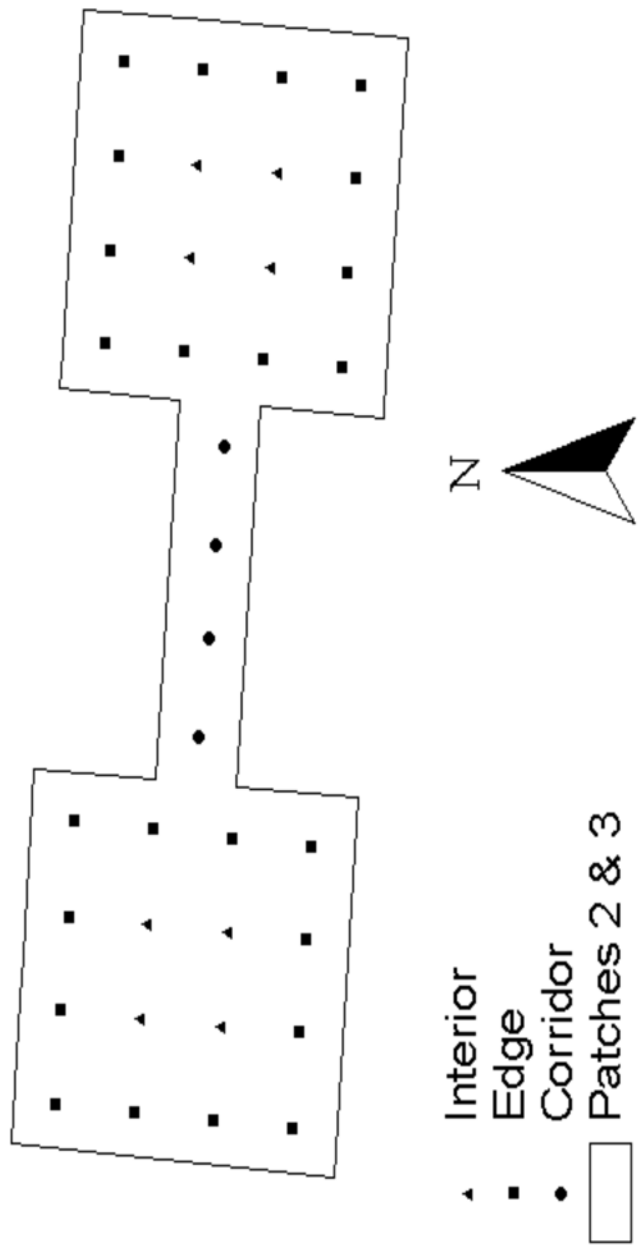
Vegetation sampling.– Vegetation sampling was conducted in patches and corridors during August 1998, 1999, and 2000. Bowne et al. (1999) reported 1997 vegetation data. Two randomly selected 4 x 4 m quadrats were established per trapping station. Total percent cover of vegetation was estimated visually. Canopy cover within the forest matrix was measured during September 2000. Densiometer readings were taken at 2 randomly selected points per trapping station; species and dbh of the nearest tree with dbh >10 cm were recorded.

Census procedures.– Live-trapping was conducted weekly March-June 1997, June-November 1998, May-December 1999, and March-November 2000. Trap stations were placed in a grid pattern (4 x 4 or 2 x 2, in large and small patches, respectively) at 32-m intervals within each patch and forest grid. Trap stations were spaced at 32-m intervals for the length of each corridor. During March 2000, 3 trapping grids were established within the forest matrix (Fig. 1.1). Each forest grid covered an area equivalent to each large isolated patch (1.6 ha). Forest grids were located at least 64 m from the edge of existing patches and corridors. Two Sherman live traps (25 x 7.5 x 7.5 cm) baited with sunflower seeds were placed within 5 m of each station and typically set for 2 consecutive nights weekly. Cotton was provided as bedding on nights when the minimum temperature was expected to fall below 10° C. Captured animals were identified to species, weighed, individually marked by toe-clipping, sexed, and the reproductive condition determined before release at the site of capture. Animal care and use procedures used were approved by the American Society of Mammalogists (1998) and the University of Georgia Animal Care and Use Committee (#A343701). Weekly population densities of each species in each patch were estimated using the minimum number alive (MNA) method (Krebs 1966). Densities were expressed as mean number of individuals•ha^{-1}•treatment^{-1}.

Habitat utilization.– Each trap location was categorized as interior, edge, or corridor. Captures at the 4 trap stations located in the center of each large patch were considered interior captures, while those at the 12 stations within 16 m of the clear-cut/forest edge were considered edge captures (Fig. 1.2). Captures in corridors were categorized as corridor captures. Only captures from large patches and connecting corridors were used in this analysis, because all traps in small patches would be considered edge traps.

Cotton mice trapped within patches and corridors were tracked using radio-telemetry during 1997 and 2000. Captured resident (>2 captures) adult cotton mice (>20 g) were taken to the laboratory and fitted with SM-1 mouse-style transmitters (AVM Instrument, Livermore, CA) attached to a collar. Animals were anesthetized with Metafane during 1997 collar fittings; a cable-tie collar mechanism used during 2000 did not require anesthesia. Animals were held in Nalgene cages and provided with food and water *ad lib* for up to 24 h, then released at the site of capture. Animals were located using a 3-element hand-held Yagi antenna and LA12-Q receiver (AVM Instrument, Livermore, CA) every 4 h during the first 72 hrs after release, then located twice nightly at 4-h intervals during 1997. During 2000, animals were located 3-5 times between 2000 and 0600 h each night. Telemetry locations were plotted on a map of the study site using ArcView 3.2 and the Spatial Movement

Figure 1.2. Diagram showing the classification of traps in large patches into interior, edge, and corridor habitat types used for habitat utilization analysis (1997-2000), Savannah River Site (SRS), Aiken County, South Carolina.


N
▲ Interior
■ Edge
● Corridor
▭ Patches 2 & 3

Analysis extension (Environmental Systems Research Institute, Redlands, CA), minimum convex polygon (MCP) home ranges were determined (Mohr 1947) and relative proportions of patch and matrix habitat types included in each home range were estimated.

Statistical analyses.– T-tests were used to compare the percentage of vegetative cover between treatments (connected vs. isolated and enriched vs. non-enriched) each year. An α level of 0.05 was used to determine significance of all statistical tests. The number of individuals captured per patch per week was used as an index of population density. These indices of density were compared using generalized estimating equations (GEE), a type of repeated-measures ANOVA (Stokes et al. 2000). Sign tests (Sokal and Rohlf 1981) were used to determine if significant trends in densities were present. General linear models (GLM) were used to determine factors explaining variation in patch population densities for each species. The primary variable was patch treatment (connected or isolated (1997-2000), or enriched or non-enriched (1999-2000)). Study year (1997-2000), percent vegetative cover, number of neighboring patches (large patches with parallel edges and separated by 128 m of matrix habitat), average temperature during the trapping period, and total rainfall during the trapping period were used to assess the influence of various abiotic (e.g., weather), biotic (e.g., vegetation), and landscape (e.g., neighboring patches) factors. SAS v. 6.0 (SAS Institute 1996) was used for these statistical analyses. Chi-square tests were used to determine if sex ratios of resident animals (captured >2 times in a treatment) or the total (residents plus animals captured only once) population of each species in each treatment differed from 1:1. Chi-square tests were used to determine if the number of captures in each habitat type (edge, interior, corridor) differed from the number expected if captures were proportional to the number of traps located in each habitat type.

RESULTS

Vegetation surveys.– Dominant species in habitat patches were oak seedlings (*Quercus* spp.), grasses (*Heterotheca* sp., *Panicum* sp., *Andropogon* sp.), smooth sumac (*Rhus glabra*), greenbrier (*Smilax rotundifolia*) and dog fennel (*Eupatorium capillifolium*). Vegetative cover was

Table 1.1. Results of t-tests comparing percent vegetative cover in connected vs. isolated and enriched vs. non-enriched patches.[1]

Year	**Treatment**	**Mean**	**SE**	**Treatment**	**Mean**	**SE**	**P**
1998	Connected	65.3	1.1	Isolated	57.9	2.0	0.001
	Enriched	31.3	3.0	Non-enriched	3.7	1.0	0.001
1999	Connected	69.9	1.4	Isolated	70.8	1.8	0.68
	Enriched	64.6	3.7	Non-enriched	28.8	3.9	0.001
2000	Connected	82.0	1.2	Isolated	79.6	1.8	0.25
	Enriched	87.1	1.8	Non-enriched	69.2	3.5	0.001

[1] Bowne et al. (1999) present 1997 vegetation data.

greater in connected (65.3%) than isolated (57.9%) patches during 1998 (Table 1.1); there were no significant differences in percent cover between connected and isolated patches during 1999 or 2000. Non-enriched patches had significantly lower mean percent vegetative cover than enriched patches during all years (Table 1.1). Dominant tree species in the forest matrix were loblolly pine, slash pine (*P. elliotii*), and willow oak (*Q. phellos*). Percent canopy cover differed significantly among the 3 forest matrix grids (ANOVA, *d.f.* = 95, $F = 15.3$, $P < 0.0001$); however, percent canopy cover was high in all grids, ranging from 94.1 ± 0.5 to 97.4 ± 0.3 (mean ± *SE*).

Drought.– This study took place during an extremely dry period. Conditions were more moist than average during 1997; a 3-year drought began during the summer of 1998 (Fig. 1.3) (NOAA 2001).

Small mammal captures.– A total of 37,500 trap nights over 4 years resulted in 1,001 captures of cotton mice, 599 of old-field mice, and 469 of cotton rats. Thirty-seven captures of golden mice (*Ochrotomys nuttalli*), 10 of southern short-tailed shrews (*Blarina carolinensis*), and 1 of the rice rat (*Oryzomys palustris*) were also recorded. Yearly trapping success ranged from 0.03 captures/trap night (1998) to 0.13 captures/trap night (1997).

Sex ratios.– Sex ratios of resident cotton rats never differed significantly from 1:1, and were only significantly different for old-field mice in isolated patches during 1997 (Table 1.2). Sex ratios of resident cotton mice deviated from 1:1 in connected, enriched, and non-enriched treatments during 1999. Sex ratios of the total cotton mouse population differed in connected patches during 1998 and 2000, and in isolated patches during 1999. In most cases, cotton mouse sex ratios were skewed toward males.

Effects of patch connectivity.– Captures of cotton rats were extremely rare during 1997; population densities never exceeded 0.5 individuals/ha in either treatment. These extremely small sample sizes precluded statistical analysis. The density of cotton rats was not significantly different between connected and isolated treatments during any year of the

Figure 1.3. Monthly Palmer Drought Severity Indices for South Carolina from January 1997-December 2000. Zero represents normal temperature and rainfall conditions; increasingly negative numbers indicate more severe drought.

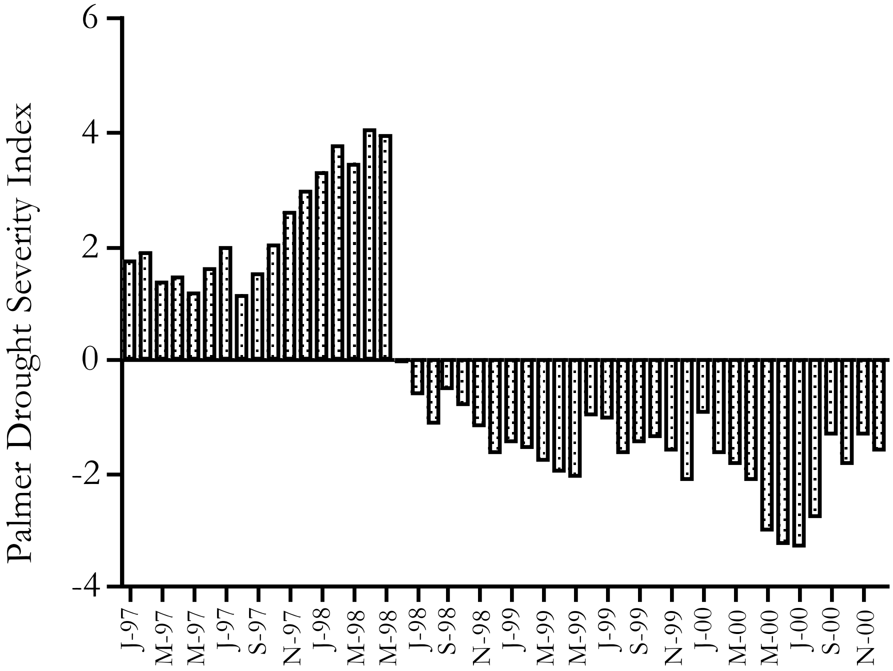
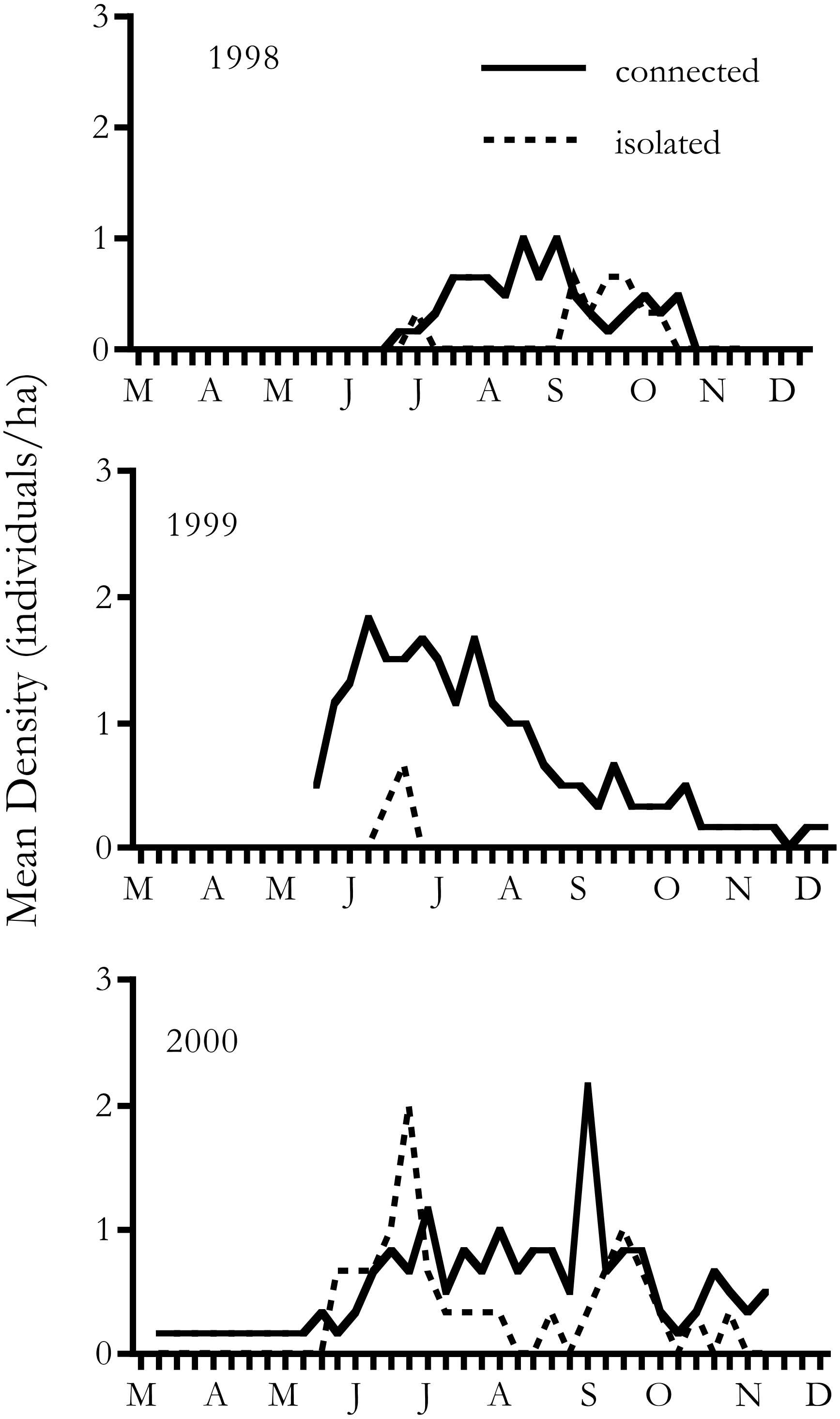

Palmer Drought Severity Index
6
4
2
0
-2
-4
J-97
M-97
M-97
J-97
S-97
N-97
J-98
M-98
M-98
J-98
S-98
N-98
J-99
M-99
M-99
J-99
S-99
N-99
J-00
M-00
M-00
J-00
S-00
N-00

Table 1.2. Sex ratios (M:F) of 3 small mammal species in each patch treatment. An asterisk (*) denotes a χ^2 value significant at $\alpha = 0.05$.

Species	**Year**	**Treatment**	**residents only**	χ^2	**total**	χ^2
S. hispidus	1997	Connected	-		-	
		Isolated	-		-	
	1998	Connected	0.83:1	0.09	1:01	0
		Isolated	-		-	
	1999	Connected	1:1	0	0.96:1	0.02
		Isolated	-		-	
	2000	Connected	1.45:1	0.93	1.31:1	0.68
		Isolated	1.33:1	0.14	0.67:1	0.4
		Enriched	1.5:1	0.2	0.75:1	0.14
		Non-enriched	-		-	
P. gossypinus	1997	Connected	0.92:1	0.08	0.9:1	0.15
		Isolated	0.76:1	0.66	0.85:1	0.32
	1998	Connected	2:1	1.33	2.15:1	5.49*
		Isolated	-		-	
	1999	Connected	2.27:1	5.44*	2.11:1	7.14*
		Isolated	1.6:1	1.19	2.33:1	4.8*
		Enriched	6:1	6*	8:1	5.44*
		Non-enriched	4.5:1	4.45*	3:1	3*
	2000	Connected	1.7:1	1.8	2.36:1	6.1*
		Isolated	1.2:1	0.9	1.6:1	0.69
		Enriched	3:1	3	4:1	4*
		Non-enriched	-		-	
P. polionotus	1997	Connected	2.75:1	3.27	2:1	2.67
		Isolated	6:1	6*	10:1	7.4*
	1998	Connected	0.5:1	0.67	1.11:1	0.52
		Isolated	-		-	
	1999	Connected	2:1	1.33	1.1:1	0.05
		Isolated	0.88:1	0.67	1:01	0
	2000	Connected	0.75:1	0.43	0.86:1	0.15
		Isolated	1:1	0	1.08:1	0.04
		Enriched	-		-	
		Non-enriched	-		-	

Figure 1.4. Trends in mean population densities (MNA) of cotton rats (*Sigmodon hispidus*) in connected vs. isolated habitat patches on the Savannah River Site (SRS), Aiken County, South Carolina.


Mean Density (individuals/ha)
1998
connected
isolated
1999
2000
0
1
2
3
M
A
M
J
J
A
S
O
N
D

study (GEE; 1998, $\chi^2 = 2.06$, $P = 0.15$; 1999, $\chi^2 = 2.19$, $P = 0.14$; 2000, $\chi^2 = 1.42$, $P = 0.23$). However, trends in MNA population densities were significant during 1998 ($P < 0.001$), 1999 ($P < 0.005$), and 2000 ($P < 0.05$). Densities tended to be higher in connected than isolated patches (Fig. 1.4). A GLM including patch treatment, percent vegetative cover, year, and the effect of individual patches explained only 39% of the variance in cotton rat population densities.

The mean density of cotton mice in connected and isolated patches was never significantly different (GEE; 1997, $\chi^2 = 1.31$, $P = 0.25$; 1998, $\chi^2 = 0.81$, $P = 0.37$; 1999, $\chi^2 = 0.01$, $P = 0.93$; 2000, $\chi^2 = 0.79$, $P = 0.37$). Trends in population density were significant during 1997 ($P < 0.05$), when densities were somewhat higher in isolated patches, and 2000 ($P < 0.005$), when densities were slightly higher in connected patches (Fig. 1.5). A GLM including patch treatment, vegetative cover, year, temperature, rainfall, and the effect of individual patches explained 66% of the variance in cotton mouse population densities.

The mean density of old-field mice was never significantly different between connected and isolated patches (GEE; 1998, $\chi^2 = 1.80$, $P = 0.18$; 1999, $\chi^2 = 0.77$, $P = 0.38$; 2000, $\chi^2 = 2.29$, $P = 0.13$). However, isolated patches tended to have somewhat higher population densities than connected patches during 1999 ($P < 0.025$) and 2000 ($P < 0.005$) (Fig. 1.6). Variance in population densities was explained by a GLM containing the variables treatment, year, individual patch effects, and vegetative cover ($R^2 = 0.61$).

Effects of habitat quality.– Population densities of cotton rats were not significantly different between enriched and non-enriched patches during 2000 (GEE, $\chi^2 = 2.00$, $P = 0.16$) (Fig. 1.7). Densities of cotton mice between enriched and non-enriched small patches were not significantly different (GEE; 1999, $\chi^2 = 0.7$, $P = 0.4$; 2000, $\chi^2 = 0.01$, $P = 0.91$); trends in densities were insignificant as well (Fig. 1.8). Only 2 old-field mice were ever captured in small patches, thus, analysis of the effects of habitat quality on this species was not possible.

Figure 1.5. Trends in mean population densities (MNA) of cotton mice (*Peromyscus gossypinus*) in connected vs. isolated habitat patches on the Savannah River Site (SRS), Aiken County, South Carolina.

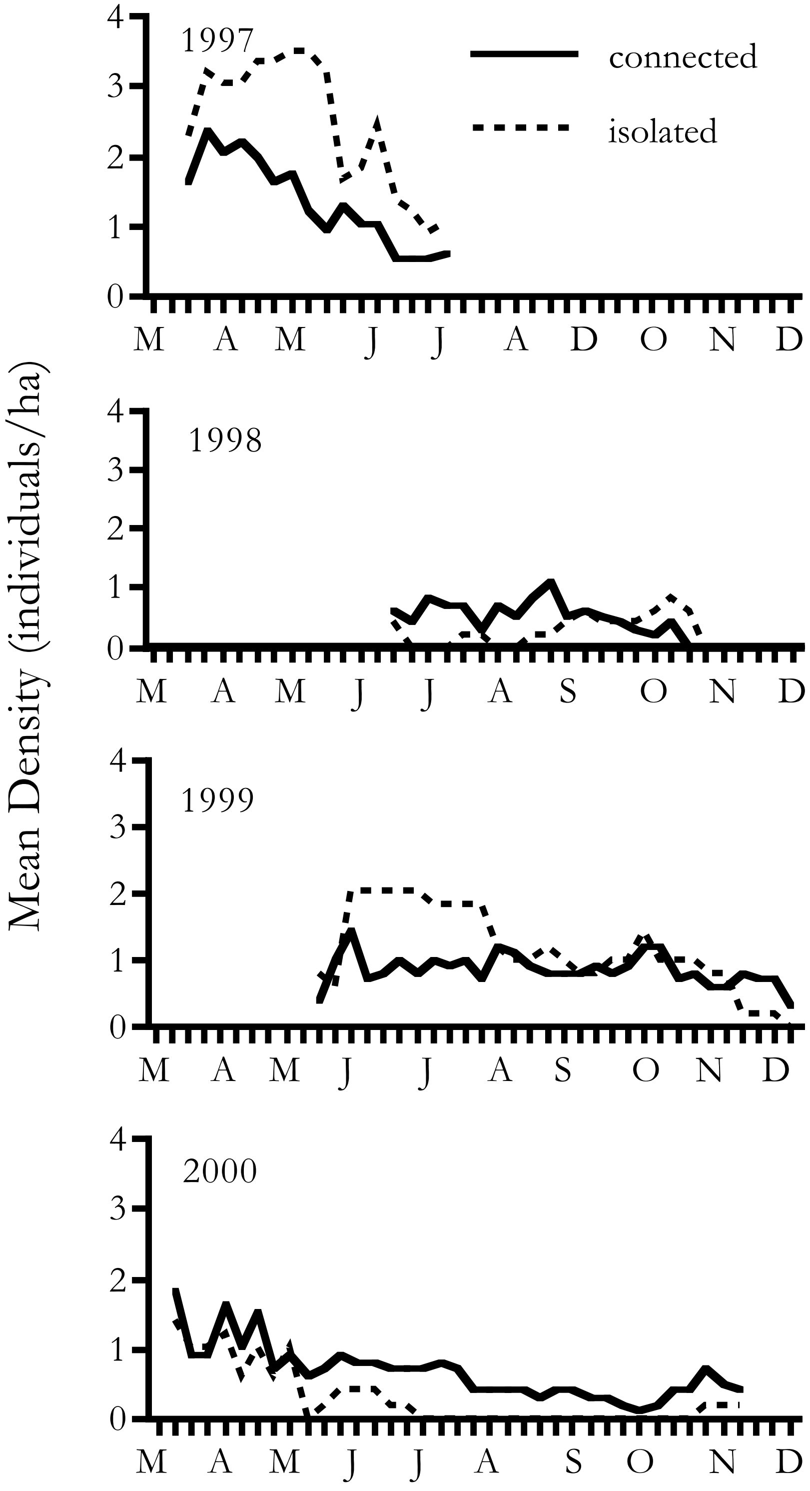

Mean Density (individuals/ha)
1997
connected
isolated
4
3
2
1
0
M A M J J A D O N D
1998
M A M J J A S O N D
1999
M A M J J A S O N D
2000
M A M J J A S O N D

Figure 1.6. Trends in mean population densities (MNA) of old-field mice (*Peromyscus polionotus*) in connected vs. isolated habitat patches on the Savannah River Site (SRS), Aiken County, South Carolina.

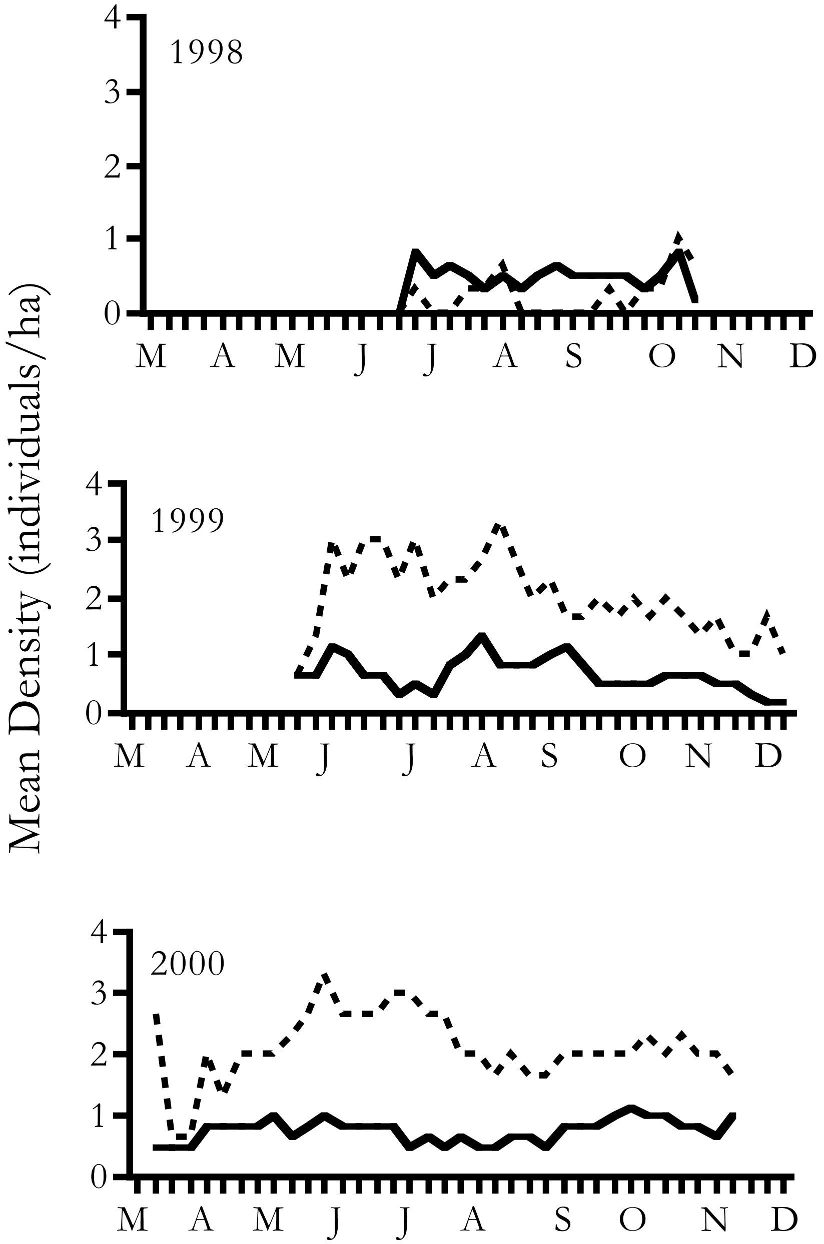

Mean Density (individuals/ha)
1998
1999
2000
0
1
2
3
4
M
A
M
J
J
A
S
O
N
D

Figure 1.7. Trends in mean population densities (MNA) of cotton rats (*Sigmodon hispidus*) in enriched vs. non-enriched habitat patches on the Savannah River Site (SRS), Aiken County, South Carolina.

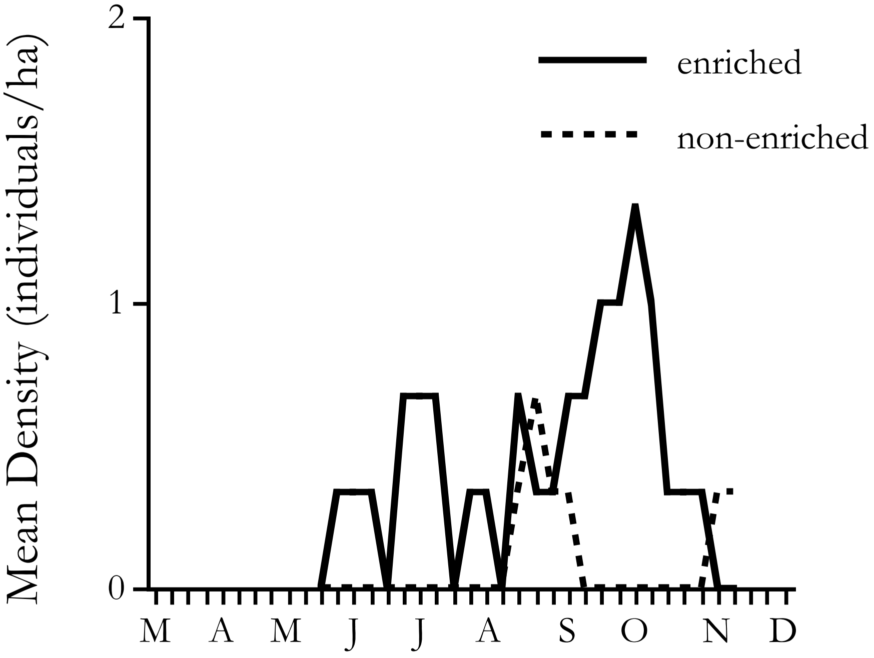

Mean Density (individuals/ha)
2
1
0
enriched
non-enriched
M
A
M
J
J
A
S
O
N
D

Figure 1.8. Trends in mean population densities (MNA) of cotton mice (*Peromyscus gossypinus*) in enriched vs. non-enriched habitat patches, Savannah River Site (SRS), Aiken County, South Carolina.

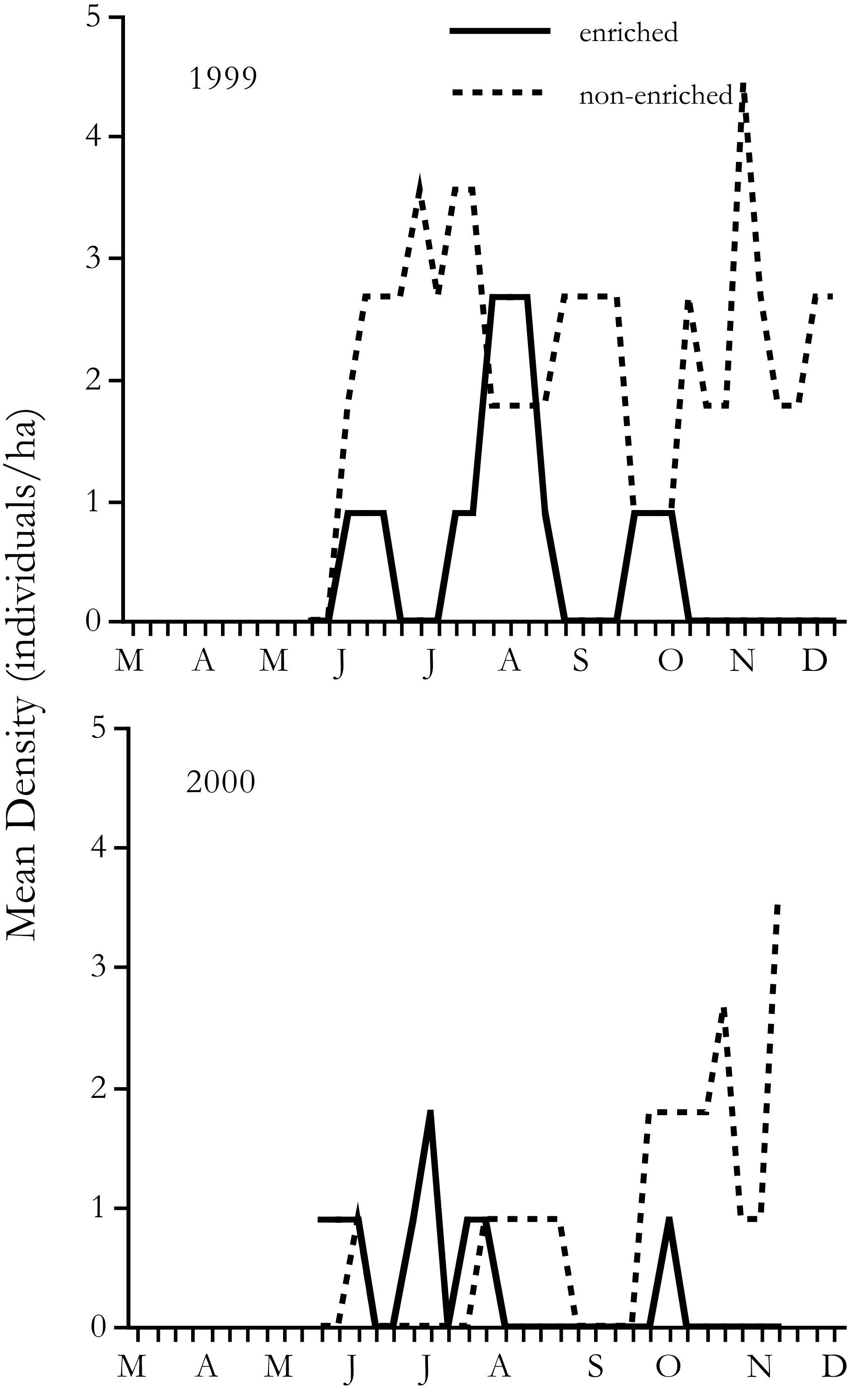

Mean Density (individuals/ha)
enriched
non-enriched
1999
2000
0
1
2
3
4
5
M
A
M
J
J
A
S
O
N
D

Table 1.3. Results of chi-square tests of the null hypothesis that small mammals are captured in interior, edge, and corridor habitat types with frequencies proportional to the number of traps in each habitat type.

Species	Year	Sex	N	*df*	χ^2	*P*
S. hispidus	1998	M	22	2	6.11	< 0.05
		F	27	2	19.7	< 0.001
	1999	M	41	2	18.84	< 0.001
		F	59	2	31.88	< 0.001
	2000	M	59	2	116.72	< 0.001
		F	107	2	110.15	< 0.001
P. gossypinus	1998	M	51	2	1.45	>0.10
		F	36	2	3.4	>0.10
	1999	M	142	2	2.9	>0.10
		F	96	2	17.33	< 0.001
	2000	M	88	2	10.26	< 0.01
		F	61	2	16.06	< 0.001
P. polionotus	1998	M	18	2	0.147	>0.95
		F	24	2	4.68	>0.05
	1999	M	67	2	25.39	< 0.001
		F	67	2	42.64	< 0.001
	2000	M	126	2	17.58	< 0.001
		F	132	2	11.5	< 0.005

Habitat utilization.– Habitat use was non-random for cotton mice and old-field mice during 1999 and 2000, and for cotton rats during all years of the study (Table 1.3). During periods of non-random habitat utilization by cotton mice (both sexes during 2000 and females during 1999), there were more captures than expected in interior traps. During 1999 and 2000, old-field mice were captured more frequently than expected in interior traps. Cotton rats were always captured more frequently than expected in connecting corridors.

The proportion of the MCP home range within patch boundaries varied greatly among individual cotton mice, ranging from 1.6% to 80.2% (mean = 39.9%) for the 12 mice radio-tracked during 1997 and 2000. Seven of the 12 home ranges included 2 habitat patches; none of these pairs of patches were connected to each other. While cotton mice obviously moved through the pine forest matrix, only 5 captures of 2 individuals were recorded during 5,700 trap nights in the forest matrix. No cotton rats or old-field mice were trapped within forest matrix habitat.

DISCUSSION

The results of this study indicate that corridors and habitat enrichment have little effect on the population densities of cotton rats, cotton mice, or old-field mice in this experimental landscape at the SRS. However, densities of cotton rats tended to be slightly higher in connected patches, while densities of old-field mice tended to be slightly higher in isolated patches. Landscape elements appeared to have even less of an effect on population densities of a habitat generalist, the cotton mouse. Landscape elements did appear to affect habitat utilization, however, as cotton rats were trapped more often than expected in corridors and cotton mice and old-field mice were trapped more often than expected in patch interiors.

Population densities.– Because we used the MNA method of population estimation, which is susceptible to bias from unequal capture probabilities among species (Slade and Blair 2000), densities of the three small mammal species in this study should not be compared to each other. The MNA method frequently underestimates population size, however, MNA estimates are a reasonable index of population size (Boonstra 1985; Slade and Blair 2000), and, unlike many population estimators, the MNA method is relatively insensitive to population size (Hilborn et al. 1976).

Peak densities of all 3 small mammal species were generally much lower than peak densities reported in other studies, but were typically within the population density ranges reported for the SRS. Cotton rat densities on the SRS typically range from 0.15 to 19.5/ha, and are highest in broomsedge (*Andropogon* sp.) and vine habitat (Golley et al. 1965). Our habitat patches most closely fit Golley et al.'s (1965) habitat type categories of broomsedge/vine, broomsedge/forb, and lespedeza. Thus our peak density of approximately 2.5/ha was within the density range reported for the SRS, but lower than expected for the preferred broomsedge habitat type. Estimates of cotton mouse population densities on the SRS range from 3.3-8.7/ha (Smith et al. 1971); Golley et al. (1965) recorded the highest densities in hardwood forests, although cotton mice were also trapped in the broomsedge habitat types. Cotton mouse population densities in our study were within the reported SRS range, with a peak density of approximately 4.5/ha. Old-field mouse densities range from 9.5-13/ha on the SRS, peaking in the lespedeza habitat type (Cothran et al. 1991); our mean peak density of 3.5/ha was much lower.

Low numbers of recaptures likely decreased out ability to detect differences in population densities between treatments. The low densities observed in our study are likely correlated with seasonal population trends in the Southeastern United States, particularly as most trapping occurred during the summer and fall months. Southeastern *Peromyscus* population densities typically peak in the spring and decline through the summer (McCarley 1954; Bigler and Jenkins 1975). A 3-year (1998-2000) drought likely decreased population densities of all 3 species; cotton mice are particularly vulnerable to water deprivation (Glenn 1970), and Eifler and Slade (1999) showed that high temperatures decreased growth of cotton rats during summer.

Deviations from a 1:1 sex ratio were rare, and only occurred in the cotton mouse and old-field mouse. This result is not surprising, however, as male-skewed sex ratios are common in *Peromyscus* spp. (Terman and Sassaman 1967) and 1:1 (Wolfe and Linzey 1977; Smith et al. 1980) and male-skewed (Bigler and Jenkins 1975) sex ratios have been reported for cotton mice. The sex ratio of old-field mice is skewed toward males at birth, but not maturity (Smith 1967). Cotton rat sex ratios have not been reported to differ significantly from 1:1 (Layne 1974; Cameron and Spencer 1981), and our results support these earlier findings.

Role of patch connectivity.– We hypothesized that population densities of all 3 small mammal species would be significantly higher in patches connected by corridors than in isolated patches. However, the difference in the number of animals captured in connected versus isolated patches was not significant. Treatment was a significant explanatory variable of variance in population densities for each species, however, other factors such as study year, vegetative cover, and patch identifier were also significant. Only cotton rats appear to have benefited from the presence of corridors. Results of this study demonstrate that response to landscape elements is species-specific, and that connected patches in an experimental landscape do not necessarily support higher population densities than isolated patches, a conclusion also reached by Davis-Born and Wolfe (2000) for gray-tailed voles (*M. canicaudus*).

Danielson and Hubbard (2000) suggest that this experimental landscape may not be properly scaled for observation of corridor effects on small mammal populations; an interpatch distance of 128 m may be too small to serve as a barrier to movement. The varying results for different small mammal species emphasize that the effect of connecting corridors is highly dependent on both the species of interest and the landscape within which it exists (Beier and Noss 1998; McIntyre and Hobbs 1999), and that the presence of a corridor is not necessarily synonymous with landscape connectivity (Tischendorf and Fahrig

2000). Habitat generalist species such as the cotton mouse are less likely to be negatively affected by landscape fragmentation.

Role of habitat enrichment.– Increased (but not statistically significant) population densities of cotton rats in small enriched patches compared to small non-enriched patches support earlier studies that found increased use of patches with experimentally enriched habitat quality (Doonan and Slade 1995; Eshelman and Cameron 1996). Lower population densities of cotton mice in enriched patches were unexpected; although habitat generalists may be able to persist in poor habitats (Adler and Wilson 1987), they should not select these habitats over higher-quality habitats. Smith et al. (1984) found that cotton mouse population densities were higher in patches to which supplemental food had been added. There are several possible explanations for our findings. Microhabitat selection may have been acting at a scale smaller than that of the patch; a patch of overall low-quality habitat still may retain small areas of ideal conditions. The CWD added to enriched patches may not have been ideal for cotton mice because it was relatively intact; cotton mice select higher decay classes of CWD (McCay 2000). However, the use of less decomposed CWD was necessary in this study, because intact logs were moved over long distances.

While vegetative cover was higher in enriched patches, the plentiful plant species, such as dog fennel, may not have been good sources of food or cover for cotton mice, and growth of vegetation may have been inhibited by drought. Because habitat quality varies with species (McIntyre and Hobbs 1999), we appear to have succeeded in increasing habitat quality for cotton rats, while the characteristics essential to high-quality habitat for cotton mice and old-field mice were absent. Peles and Barrett (1996) found that while reduced vegetative cover negatively affected population density and recruitment of meadow voles, increased cover did not result in significantly higher densities than those found in control patches. Perhaps we did not significantly affect population densities by addition of cover; removal of cover may have been a more influential treatment.

Conspecific attraction of cotton mice may also have influenced patch occupation (Smith and Peacock 1990). The presence of conspecifics may be more important than intrinsic habitat quality in patch selection when animals exist at low population densities (Greene and Stamps in press); naïve animals may use conspecifics as cues to habitat suitability, choosing to settle in areas that are already occupied rather than moving on into unknown territory (Smith and Peacock 1990). Enriched patches may have been suitable for colonization by cotton mice, however, mice may have settled in patches that were already inhabited rather than move on to empty patches (Greene and Stamps in press).

Role of patch size.– Captures in small (0.4-ha) patches were relatively rare, thus our ability to draw conclusions about the effects of patch size on the small mammals at this site was limited. However, when animals were captured in small patches (1999 and 2000), population densities of cotton mice and cotton rats were often higher in small (0.4-ha) than large (1.6-ha) patches. However, this result may be an artifact of patch size (Gaston et al. 1999); a single animal known alive in a small patch resulted in a much higher density than a single animal known alive in a large patch. These results do, however, support a negative density-area relationship for cotton rats (Smith and Vrieze 1979), and a negative or neutral relationships for various *Peromyscus* spp. (Bowers and Matter 1997).

Habitat utilization.– We predicted that cotton mice would use all habitat types equally; this hypothesis was rejected as cotton mice selected interior traps during 1999 and 2000 and were captured very infrequently in the forest matrix. While all 3 small mammal species considered in this study moved through matrix habitat, few (if any) animals were resident in the pine forest matrix. Placement of forest trapping grids toward the edges of the study site may have influenced our ability to detect animals moving within the matrix.

Non-random use of landscape elements was expected for old-field mice and cotton rats, as these species are more restricted to a particular habitat type. Old-field mice were, as expected, captured more often in patch interiors. Cotton rats were unexpectedly captured most frequently in corridors. These results suggest that cotton rats use corridors as permanent home ranges as well as movement routes (Rosenberg et al. 1997, Danielson and Hubbard 2000). The potential for animals becoming resident within corridors must be considered when corridor length and width are selected.

The results of this study suggest that landscape elements have greater effects on the population dynamics of habitat specialists, such as the cotton rat and old-field mouse, than on habitat generalists, such as the cotton mouse. Further studies of the effects of habitat fragmentation at multiple scales and on a range of species varying in degree of habitat specialization are needed.

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CHAPTER 2

EFFECTS OF LANDSCAPE STRUCTURE ON HOME RANGE SIZES AND INTERPATCH MOVEMENTS OF THREE SMALL MAMMAL SPECIES

ABSTRACT

Corridors are predicted to benefit populations in patchy habitats by promoting movement, thus increasing population densities, gene flow, and recolonization of extinct patches. However, few investigators have considered use of the total landscape, including patches, corridors, and the habitat matrix, by small mammals. This study compared home range sizes and movements from connected and isolated patches for 3 species of small mammals, the cotton mouse (*Peromyscus gossypinus*), old-field mouse (*P. polionotus*) and cotton rat (*Sigmodon hispidus*). The presence of a corridor did not significantly influence home range size, but did increase the probability of emigration from a patch by cotton mice and old-field mice. The high proportion of animals moving between and among patches that were isolated from each other suggests that corridor connectivity was unnecessary for small mammals in this particular landscape.

Key words: corridor, fragmentation, landscape, matrix, movement, *Peromyscus gossypinus, Peromyscus polionotus, Sigmodon hispidus*

INTRODUCTION

Of the 4 fundamental processes affecting population dynamics (birth, death, immigration and emigration), immigration and emigration are the most difficult to measure, and have frequently been ignored by ecologists (Turchin 1998). Yet movements of individual animals have great potential to affect population dynamics (Kozakiewicz 1993), particularly in fragmented landscapes, by the exchange of individuals and their genetic information among habitat patches. Inclusion of corridors to increase movement through fragmented landscapes has become common in conservation and land management plans (Rosenberg et al. 1997); however, neither the actual use of corridors nor movement through the "hostile" matrix surrounding suitable habitat patches has been frequently quantified (Beier and Noss 1998). Gascon et al. (1999) found that species capable of using the habitat matrix were more likely to persist in a fragmented landscape than species confined to remnant habitat patches. Thus, utilization of the landscape matrix may be a key component of survival in fragmented landscapes (Gascon et al. 1999). Previous studies have sought to determine the characteristics of corridors (i.e., corridor width, length, quality, or gaps) that influence utilization without evaluating the underlying assumption that movements are in fact more frequent through corridors than through matrix habitat (e.g., Ruefenacht and Knight 1995; Andreassen et al. 1996b; Bright 1998). The assumption that corridors increase interpatch movement rates remains largely untested. With the limited data available, it is difficult to determine not only if a corridor is necessary for the persistence of a particular species or population, but also if a corridor would actually increase landscape connectivity and movement rates.

Connectivity is meaningful only in the context of a particular species in a particular landscape; Tischendorf and Fahrig (2000) make the important distinction between corridors and connectivity. The presence of a corridor in a landscape does not necessarily mean that the landscape has high connectivity, nor does the absence of corridors mean that it does not. A fragmented landscape with no corridor connections between patches may be highly connected if the species in question is capable of moving through the particular matrix habitat between patches (McIntyre and Hobbs 1999; Renjifo 2001).

The relative ability of an organism to move through different types of matrix habitat is another important component of connectivity that is frequently overlooked (Pither and Taylor 1998; Ricketts 2001). The analogy of terrestrial habitat matrix to an impassable "ocean" is derived from island biogeography theory (MacArthur and Wilson 1967), which relates species diversity to island size and distance from the "mainland," and has long influenced metapopulation theory. However, the matrix separating habitat patches is more likely to act as a "selective filter" than an absolute barrier to movement (Gascon et al. 1999). The capability of an animal to move between and among habitat patches is affected by multiple factors, including size of the animal (Danielson and Anderson 1999), degree of fragmentation of the landscape (Andrén 1994), isolation of or distance between patches (Kozakiewicz 1993), type of landscape matrix separating habitat patches (Åberg et al. 1995; McIntyre and Hobbs 1999), and potential behavioral aversions to movement through the edges between habitat types (Stamps et al. 1987; Haddad 1999; Lidicker 1999, Ricketts 2001). Unfortunately, the behavior of animals in large-scale fragmented landscapes has not been thoroughly addressed (Yahner and Mahan 1997). The effects of matrix habitat on small mammal movement behavior remain unclear.

One of the key arguments for establishing corridors between patches is that corridors increase successful movements between habitat patches (Rosenberg et al. 1997). Many investigators have shown that population demographics are affected by corridors (e.g., increased genetic heterozygosity in connected patches, Aars and Ims 1999; increased population density in connected patches, Haddad 1999), that animals utilize a particular corridor (Lorenz and Barrett 1990; Beier 1993; Downes et al. 1997), or that mortality during movement is higher in an extremely hostile experimental matrix than in a corridor (Aars et al. 1999). However, few have actually shown increased movement rates between connected patches as compared to isolated patches. While the number of cotton rats leaving connected and isolated patches was not significantly different, Bowne et al. (1999) found that proportionally more individuals left connected patches through corridors than would be expected based on corridor width alone. Only Haddad (1999) has reported significant positive effects of corridors on movement rates. Numerous studies have actually found that corridors do not significantly increase interpatch movements of small mammals. For example, while nearly twice as many gray-tailed voles (*Microtus canicaudus*) in connected than isolated patches changed patches, the differences were not significant for either males or females (Davis-Born and Wolff 2000). Aars and Ims (1999) found extremely low interpatch transfer rates for root voles (*M. oeconomus*), however, increased genetic heterozygosity in connected patches lead them to suspect short-term mating excursions into corridors. La Polla and Barrett (1993) determined that meadow voles (*M. pennsylvanicus*) disperse more often between connected than isolated patches; however, they also found no difference in the number of voles dispersing among treatments. While Andreassen et al. (1996a) determined an optimal width for corridors connecting vole populations, no "control" treatment (no corridor) was included, so it is not known if movement rates between connected patches may have been greater than movement rates between isolated patches. At the site of the current study, Danielson and Hubbard (2000) unexpectedly found that the presence of a connecting corridor decreased the dispersal probability of old-field mice (*Peromyscus polionotus*).

We investigated the influence of patch connectivity on home range sizes and interpatch movements of 3 small mammal species, the cotton mouse (*P. gossypinus*), the old-field mouse, and the cotton rat (*Sigmodon hispidus*) in an experimentally fragmented landscape. Because *Peromyscus* home range sizes are inversely proportional to population density (Wolff 1985), and densities at this site were extremely low, it is unlikely that home range size was limited by competition with conspecifics. We hypothesized that increased movement should lead to larger home range sizes of all 3 study species in connected rather than in isolated patches. As cotton mice are considered habitat generalists, while the other 2 species are more restricted to open areas, such as the clear-cuts used in this study (Golley 1965; Danielson and Anderson 1999), we predicted that cotton mice would move more frequently among patches that were not connected to each other than would the other 2 species.

MATERIALS AND METHODS

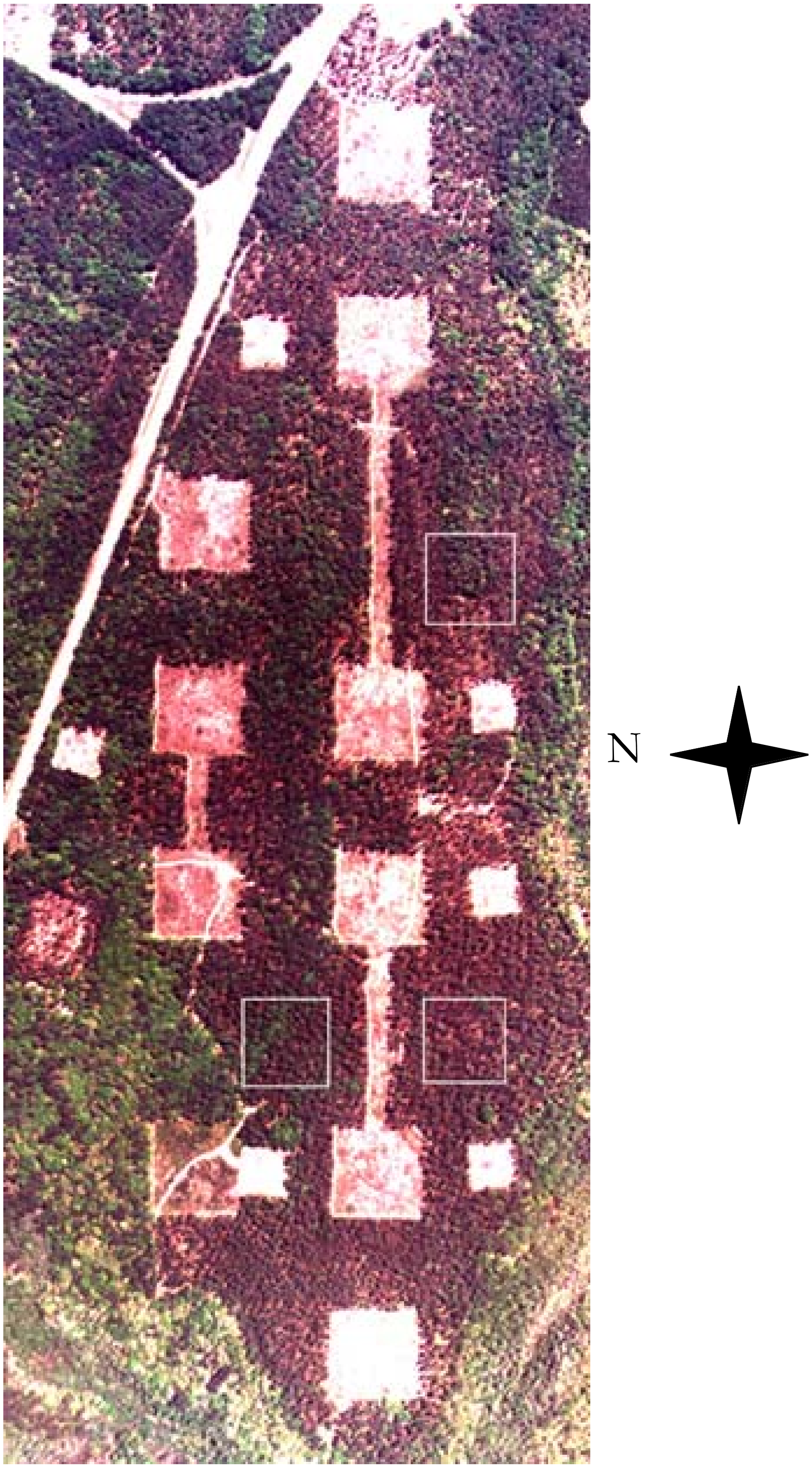
Study site.– The study was conducted on the Savannah River Site (SRS) in Aiken County, South Carolina (33°0-25' N, 81°25-50' W). The study site was an experimentally fragmented landscape (approximately 110-ha) of clear-cut patches embedded within a managed loblolly pine (*Pinus taeda*) forest. Four patch treatments were included in the design:

large (1.6 ha) connected (n=3), large (1.6 ha) isolated (n=3), small (0.4 ha) isolated experimentally enriched (n=3), and small (0.4 ha) isolated non-enriched (Fig. 2.1). Each replicate of the connected treatment consisted of 2 large patches linked by a 32-m wide corridor of length 128, 256, or 384 m. Large patches were established in 1994-1995 by clear cutting and burning (Haddad 1999); small patches were established in 1998 by the same methods. All patches were burned and seeded with *Lespedeza cuneata* in 1998 to return each to a similar stage of secondary succession. During March 2000, 3 grids, each the same size as a large isolated patch (1.64 ha), were established in the forest matrix (Fig. 2.1).

Live-trapping and radio-telemetry.– Live-trapping was conducted during March-June 1997, June-November 1998, May-December 1999, and March-November 2000. Trap stations were placed at 32-m intervals within each patch, corridor, and forest grid (16 stations/large patch; 4 stations/small patch). Two Sherman live traps (25 x 7.5 x 7.5 cm) baited with sunflower seeds were placed within 5 m of each station marker and typically set for 2 consecutive nights weekly. Cotton was provided as bedding when minimum temperature was expected to fall below 10^{o} C. Captured animals were identified to species, sexed, weighed, marked by toe-clipping, and the reproductive condition determined before release at the site of capture. All animal care and use procedures were approved by the American Society of Mammalogists (1998) and the University of Georgia Animal Care and Use Committee (#A343701).

Home range analysis.– During fall 1997 and summer 2000, resident (>3 captures) cotton mice (n=13) were fitted with radio collars (AVM Instrument, Livermore, CA) and located using a 3-element hand-held Yagi antenna and LA12-Q receiver (AVM Instrument, Livermore, CA) for 10 days. Captured animals were housed in Nalgene cages and provided with food and water *ad lib* until release. During 1997, animals were anesthetized with Metofane during collar fitting; the cable-tie collar mechanism used in 2000 did not require anesthesia. Mice were allowed to acclimate to collars for approximately 24 h before release at the site of capture. The Universal Transverse Mercator (UTM) coordinates of trap stations were recorded using a Geographic Positioning System (GPS) unit, and cotton mice were

Figure 2.1. Aerial photograph (1999) of the experimentally fragmented landscape on the Savannah River Site (SRS), Aiken County, South Carolina. Each large patch was 128 x 128 m and each small patch was 64 x 64 m. Locations of forest matrix trapping grids are outlined in white.


N

located by triangulation from these known locations at 4-h intervals for the first 72 h and twice nightly at 4-h intervals for the next 7 days during 1997. Mice were located 3-4 times nightly between 2000 and 0600 h during 2000.

Home range sizes were estimated from live-trapping records for cotton rats and old-field mice during 2000 (March-November), and for cotton mice during both 1997 and 2000 (March-June). Cotton mouse home ranges were also estimated using radio-telemetry. Captures of all species were too low to allow for home range analysis during 1998 or 1999. Home range sizes were estimated using the minimum convex polygon (MCP) method (Mohr 1947), in the computer program CALHOME (Kie et al. 1996). Home ranges were estimated for all adult animals with >3 captures. Animals were categorized by the type of patch utilized over the trapping season, connected or isolated. Some individuals were trapped within patches from both treatments; these animals were considered to have used multiple patch types.

Interpatch movements.– Animals that were captured >2 times as adults were included in analysis of interpatch movement. Juvenile animals were eliminated from analysis due to insufficient captures to allow for satisfactory consideration of natal dispersal events. The proportion of animals of each species that were captured outside the patch of initial adult capture was determined. Animals were categorized by the treatment of the patch of original adult capture (connected or isolated).

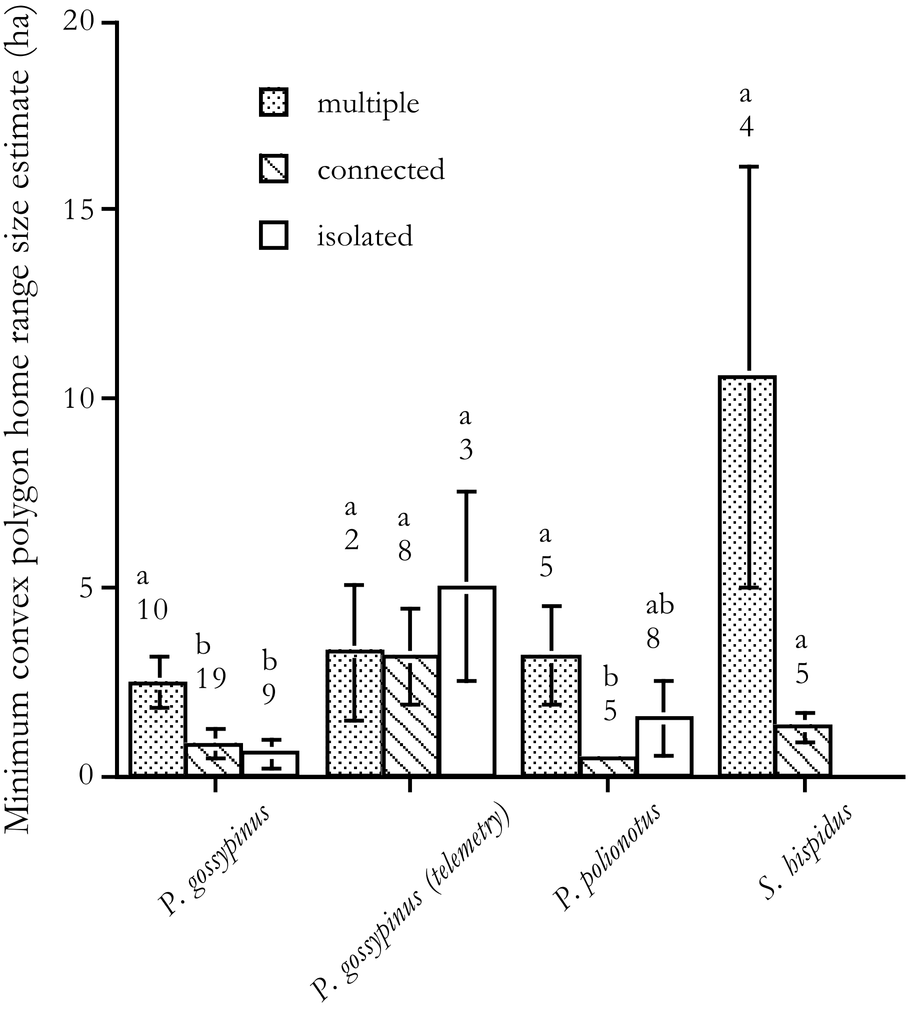
Maximum movement distances.– The straight-line distance between the 2 most distant points of capture was calculated for all adults that were captured more than once. Each animal was categorized by patch and treatment of initial capture, sex, and year.

Statistical analyses.– As home range estimates were not normally distributed, they were normalized by log-transformation prior to analysis (Ott 1993) using SAS v. 6.0 (SAS Institute 1996). Treatment effects were detected using t-tests (cotton rats) or analysis of variance (ANOVA) followed by Scheffé pair-wise comparisons if significant differences were evident (*Peromyscus* spp.). Because there was no significant effect of sex on home range size for any species, or of year on cotton mouse mean home range size ($P > 0.05$), data were pooled by sex and year. Chi-square tests were used to compare the proportion of adults that moved from the patch of initial adult capture. Logistic regression models predicting the probability of interpatch movement were constructed for cotton mice during 1997, 1999, and 2000, and old-field mice during 1999 and 2000. Factors considered in the logistic regression models (PROC LOGISTIC) were sex of the animal, population density of the patch of origin (determined using the minimum number alive (MNA) method, Krebs 1966), treatment of the patch the animal emigrated from, and individual patch number. Analysis of variance was used to determine if the average maximum distance moved by each species was significantly affected by treatment, sex, or year.

RESULTS

Home range sizes.– Home range sizes of cotton mice that utilized multiple habitat patch types (2.5 ± 0.7 ha) (Mean ± *SE*) were greater than those of individuals that utilized only 1 patch type (connected: 0.9 ± 0.4 ha, isolated: 0.6 ± 0.4 ha) (Scheffé pair-wise comparisons, *d.f.* = 34, $F = 3.28$, $P < 0.05$); however, home range sizes of cotton mice that used either only connected or only isolated patches were not different from each other (Fig. 2.2, Scheffé pair-wise comparisons, *d.f.* = 34, $F = 3.28$, $P > 0.05$). Home range sizes of radio-tracked cotton mice from the different categories were not different (ANOVA, *d.f.* = 2, $F = 0.51$, $P = 0.62$) (Fig. 2.2). Home range sizes calculated using radio-telemetry locations were larger (3.4 ± 0.9 ha) than those calculated from trap locations (1.7 ± 0.4 ha) (ANOVA, *d.f.* = 1, $F = 13.44$, $P < 0.001$). Home range sizes of old-field mice using multiple patch types were larger (3.2 ± 1.3 ha) than those of animals using only connected patches (0.5 ± 0.1 ha) (Scheffé pair-wise comparisons, *d.f.* = 15, $F = 3.68$, $P < 0.05$). However, home ranges sizes for old-field mice using only isolated patches (1.5 ± 1.0 ha) were not different from those of mice using either multiple patch types or only connected patches (Fig. 2.2). Home range sizes of cotton rats that utilized patches from both connected and isolated treatments (10.6

Figure 2.2. Average minimum convex polygon home range sizes of 3 small mammal species captured in an experimentally fragmented landscape on the Savannah River Site (SRS), Aiken, South Carolina. Numbers above columns indicate sample size, and columns with different letters are significantly different from each other at $P < 0.05$ (within species comparisons only.)


Minimum convex polygon home range size estimate (ha)
20
15
10
5
0
multiple
connected
isolated
a
10
b
19
b
9
a
2
a
8
a
3
a
5
b
5
ab
8
a
4
a
5
P. gossypinus
P. gossypinus (telemetry)
P. polionotus
S. hispidus

± 5.6 ha) were not larger than those of animals that only used connected patches (1.3 ± 0.4 ha) (Fig. 2.2, t-test, *d.f.* = 7, $T = 1.41$, $P > 0.2$). No cotton rats used only isolated patches.

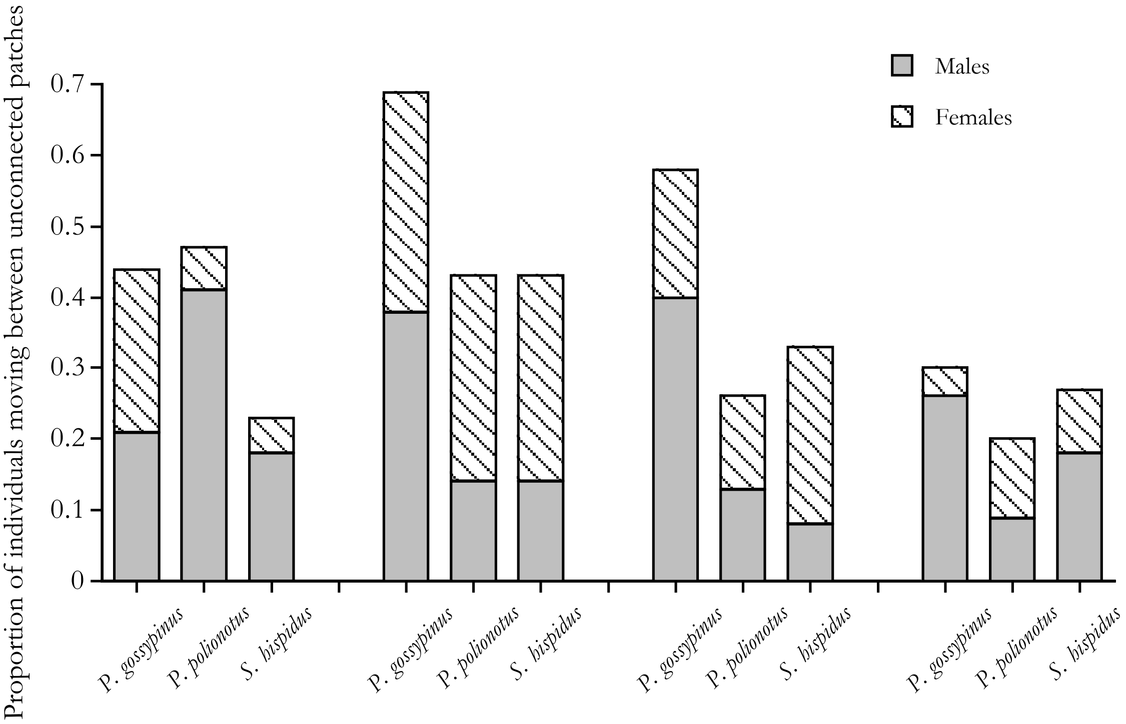
Interpatch movements.– Logistic regression models adequately predicting the probability of an individual emigrating from a patch could not be constructed for old-field mice during any year or for cotton mice during 1997 or 1999. The model predicting emigration from a patch by cotton mice during 2000 was significant ($P = 0.02$), but the individual variables included (treatment, $P = 0.1$; patch identifier, $P = 0.1$; population density, $P = 0.15$; sex, $P = 0.16$) were not.

Data from each sex were combined for chi-square analysis of the null hypothesis that the proportion of small mammals moving from connected patches would be the same as the proportion moving from isolated patches. Cotton mice moved from connected patches more frequently than expected only during 1999 (Table 2.1). Old-field mice moved from connected patches significantly more often than expected during both 1999 and 2000. Sample sizes of all 3 species were insufficient for analysis during 1998, and sample sizes of cotton rats were never large enough to allow for analysis of interpatch movements. During 1998-1999, proportionally more cotton mice than the other 2 species moved between unconnected patches (Fig. 2.3). During 1997, a higher proportion of old-field mice moved between unconnected patches. The proportions of old-field mice and cotton rats moving between unconnected patches were similar during 1998-1999 (Fig. 2.3). The total proportion of individuals of each species making interpatch moves was similar during 2000. During 1997 and 2000, proportionally more males than females of each species moved between unconnected patches, while the opposite was true during 1998 and 1999 (Fig. 2.3). *Maximum distance moved.*– The maximum distance moved by cotton mice was affected by year (ANOVA, *d.f.* = 3, $F = 2.90$, $P = 0.04$) but not treatment (ANOVA, *d.f.* = 2, $F = 1.57$, $P = 0.21$) of the patch of initial adult capture (Fig. 2.4). The average maximum distance moved was however, typically shorter (range 100-360 m) for those animals initially captured in a

Table 2.1. Results of chi-square tests of the null hypothesis that the proportion of *Peromyscus* spp. moving from connected patches is not significantly different from the proportion moving from isolated patches.

Species	Year	Observed	Expected	df	χ^2	p
P. gossypinus	1997	12	14	1	0.28	>0.05
	1998	2	-	-	-	-
	1999	13	6.3	1	7.22	< 0.05
	2000	8	4.5	1	2.72	>0.05
P. polionotus	1997	5	2.7	1	2.06	>0.05
	1998	-	-	-	-	-
	1999	4	0.5	1	24.5	<0.05
	2000	6	1.7	1	11.11	< 0.05

Figure 2.3. Proportion of individuals of each species captured >2 times that moved between habitat patches unconnected to each other. Numbers above each column indicate sample size.


Proportion of individuals moving between unconnected patches
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Males
Females
P. gossypinus
P. polionotus
S. hispidus
P. gossypinus
P. polionotus
S. hispidus
P. gossypinus
P. polionotus
S. hispidus
P. gossypinus
P. polionotus
S. hispidus

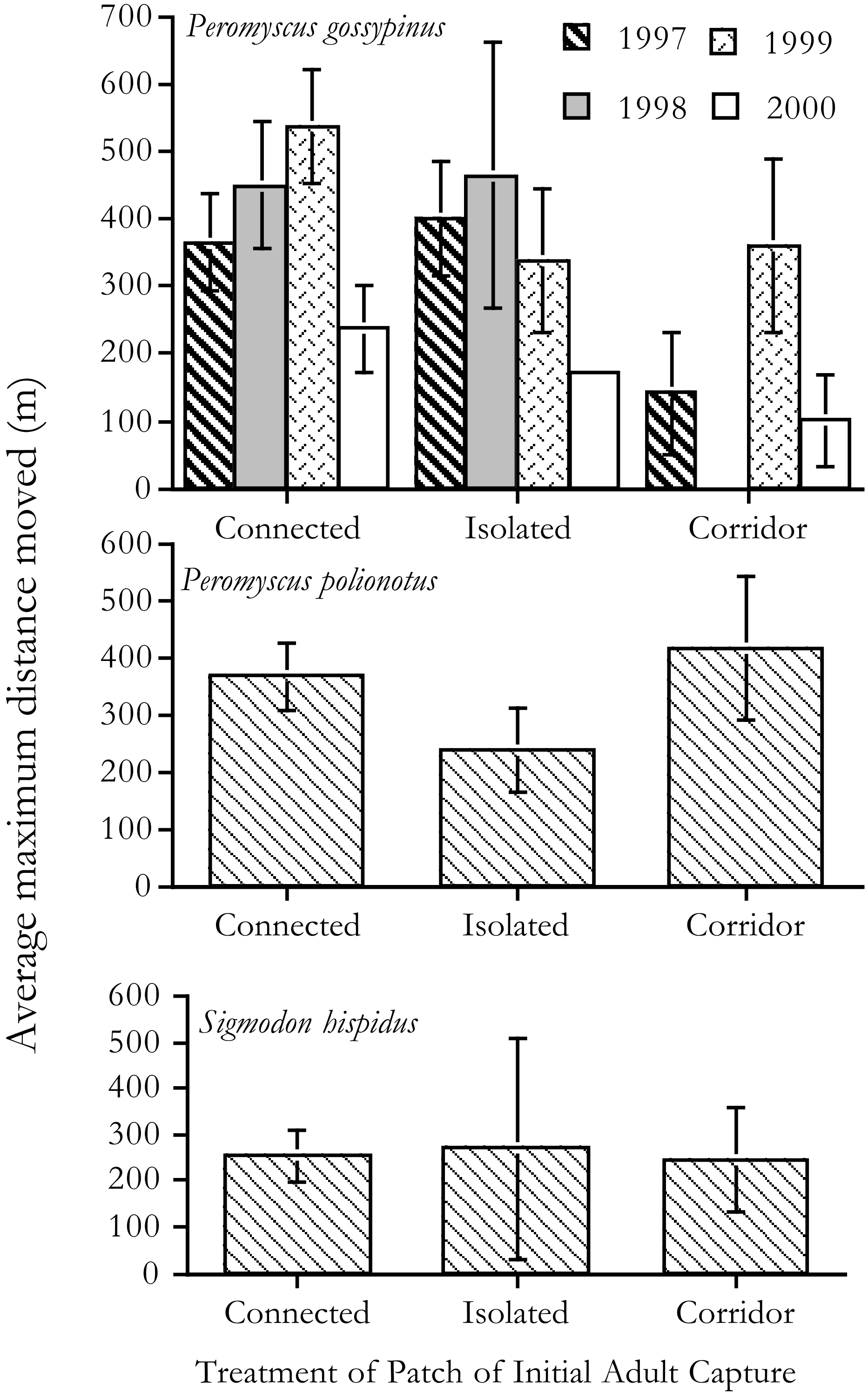
corridor than for those first captured in either connected (240-540 m) or isolated patches (170-460 m). Maximum distances moved by old-field mice were not affected by year,sex, or treatment (ANOVA, *d.f.* = 6, *F* = 0.73, *P* = 0.63) (Fig. 2.4), although those animals first captured in isolated patches moved least (238.6 ± 73.2 m) and those first captured in corridors moved farthest (417.6 ± 126.9 m). The average maximum distance moved by cotton rats was approximately 250 m regardless of treatment (Fig. 2.4). Distances moved by cotton rats were not affected by year, sex, or treatment (ANOVA, *d.f.* = 5, *F* = 0.16, *P* = 0.98).

DISCUSSION

Home range sizes.– The use of the MCP method of calculating home range size has been debated (Harris et al. 1990; White and Garrott 1990); however, because the number of locations per animal was limited in this study, the MCP method was the most robust for our purposes (Harris et al. 1990). Small mammal home range sizes tend to increase with sample size, approaching an asymptote at 4 (Bowers et al. 1996) or 9 captures (Krohne 1986). Due to limited numbers of recaptures, we calculated home ranges for adult animals captured >4 times. When MCP area was plotted against the number of locations, no clear pattern of increasing home range size was observed, nor were home ranges sizes observed to approach an asymptote with increasing sample size (*personal observation*).

Our mean home range size of 2.5 ± 0.7 ha (mean ± *SE*) calculated from trapping records for cotton mice utilizing multiple patch types was larger than ranges reported earlier (0.18-0.81 ha) (Wolfe and Linzey 1977). Larger home range sizes in our study may be a result of landscape fragmentation; individuals may range over a wider area to obtain necessary resources in a fragmented habitat (Collins and Barrett 1997). Individuals using only 1 patch type had an average home range size of 0.9 ± 0.4 ha in connected patches and 0.6 ± 0.4 ha in isolated patches; these average home range sizes were similar to those previously reported (Wolfe and Linzey 1977). Trapping grid size also affects home range size estimates; our estimates are conservative due to trap placement, because home ranges likely extend beyond

Figure 2.4. Average maximum distances (± 1 *SE*) moved by each species of small mammal trapped on the Savannah River Site (SRS) during 1997-2000. Average maximum distance was calculated as the average of the distance between the 2 farthest points of capture for each individual.


Average maximum distance moved (m)
Peromyscus gossypinus
1997
1998
1999
2000
700
600
500
400
300
200
100
0
Connected
Isolated
Corridor
Peromyscus polionotus
600
500
400
300
200
100
0
Connected
Isolated
Corridor
Sigmodon hispidus
600
500
400
300
200
100
0
Connected
Isolated
Corridor
Treatment of Patch of Initial Adult Capture

the areas trapped (Hayne 1949). While traps were placed relatively far apart (32 m) in this study, this trap placement was necessary to keep trapping effort manageable on such a large study site. Another potential explanation for the large home range estimates of animals using multiple patch types is that these animals were predominantly male, which tend to have larger home ranges than females (Stickel 1954). Those using only connected or isolated patches were more evenly distributed between the sexes.

Cotton mouse home ranges calculated from telemetry locations were larger than those calculated from trapping records, ranging from 3.2 ± 1.3 ha (animals utilizing connected patches) to 5.0 ± 2.5 ha (isolated patches), despite collection over a shorter period of time (≤10 days). These home ranges are likely larger than trap-revealed home ranges because telemetry allows for location of animals outside the area trapped, especially in the forest matrix. Telemetry also allows for multiple locations of an animal during a night; a trapped animal cannot continue to move across the landscape, only 1 location can be recorded per night, and movement behavior may be altered because animals spend a great deal of time in traps (Kozakiewicz and Szacki 1995). When possible, radio-telemetry rahter than live-trapping should be used to estimate home ranges.

Home ranges reported for old-field mice vary widely; 0.34 ± 0.02 to 10.66 ± 1.46 acres (0.14 ± 0.01 to 4.32 ± 0.6 ha) (Stickel 1954). Home range sizes average 0.14 ha on the SRS (Cothran et al. 1991). Thus our values of 0.52 ± 0.1 to 3.21 ± 1.3 ha are within the expected range. Larger home ranges for animals using both patch types could be influenced by sex of the animals; 4 of the 5 old-field mice using both patch types were female, the sex reported to have larger home range sizes in this species (Stickel 1954). Recapture frequency did not affect home range size of old-field mice; animals located in multiple patch types were captured fewer times on average than those captured in only 1 patch type.

Home ranges of cotton rats have been reported to range from 0.16 (female) to 0.39 ha (male) (Cameron and Spencer 1981, 1985), with the ranges of females generally smaller than those of males (Cameron and Spencer 1985). Home ranges in this study were much larger than those reported in these earlier studies, ranging from 1.3 ± 0.4 ha (connected patches) to 10.6 ± 5.6 ha (both patch types). These results are likely skewed by the large home ranges (25.1 and 13.4 ha) of 2 adult male cotton rats that moved over the entire study area. As we could only estimate a small number (n=9) of home ranges, and it was not possible to separate the influence of sex on home range size, the results for cotton rat home range sizes should be interpreted with caution.

Interpatch movements.– Peromyscus spp. moved from connected patches more often than expected when compared to movement from isolated patches (cotton mice, 1999; old-field mice, 1999 and 2000). These results support the theory that corridors promote movement, particularly for habitat specialists such as the old-field mouse (Danielson and Anderson 1999). Corridors also increased movement (though not always significantly) of root voles (*M. oeconomus*) (Andreassen et al. 1998; Aars and Ims 1999), gray-tailed voles (*M. canicaudus*) (Davis-Born and Wolfe 2000), and meadow voles (*M. pennsylvanicus*) (La Polla and Barrett 1993) between connected habitat patches. At the site of the current study, corridors were the preferred route of exit for transplanted cotton rats leaving connected patches (Bowne et al. 1999). However, the results of our study contradict those of Danielson and Hubbard (2000), who found that transplanted old-field mice were less likely to leave connected than isolated patches, although their conclusion was weakly supported.

The design of the experimental landscape may have influenced our ability to detect movement from isolated patches. Animals that disappeared from a patch could only be confirmed to have emigrated rather than died when they were recaptured in a different patch. While connected patches were located toward the center of the study area and were adjacent to between 1 and 4 other patches, all isolated patches were located toward the ends of the study area and bordered just 1 other large patch (Fig. 2.1). Thus, the possibility that animals moved from isolated patches without detection is high. The true proportion of animals moving from connected patches may not have been greater than the proportion of animals moving from isolated patches. While several animals moved between connected patches, conceivably via corridors, many of these same animals also moved between isolated patches. The high proportion of animals moving between patches isolated from each other suggests that the interpatch distance of 128 m was insufficient or that matrix habitat was not of poor enough quality to deter movements by these small mammals.

Danielson and Anderson (1999) suggest that body size is more important than habitat specialization in determining the size of a "species-specific landscape;" larger animals should be able to move farther, regardless of habitat specialization. Variation in the proportion of small mammals of each species moving between unconnected patches in our study provides mixed support for both their body-size and habitat-specialization hypotheses. The cotton mouse, a generalist that is intermediate in body size, moved between unconnected patches more frequently than the other 2 species. However, the proportion of old-field mice and cotton rats moving between unconnected patches was similar during all 4 years of the investigation (Fig. 2.3), and the average maximum distance moved by cotton mice and cotton rats was similar (Fig. 2.4). As adult cotton rats are approximately 5-10 x larger than adult *Peromyscus*, these results contradict the hypothesis that larger animals will move farther and more frequently than smaller animals (Danielson and Anderson 1999).

The decrease in the proportion of all species moving between unconnected patches with time appeared to reflect the increase in habitat quality as clear cuts aged and vegetative cover increased. During the first few years of secondary succession, as patches increase in age and habitat quality, these patches should be able to support more animals and small mammals likely have less incentive to emigrate in search of better habitat. Danielson and Anderson (1999) found greater numbers of cotton mice and cotton rats in 3-year-old stands than in 2-year-old stands, and greater numbers of all 3 species in 2-year-old compared to 1-year-old stands. However, since old-field mice prefer open habitat (Golley et al. 1965), the decreasing proportion of this species moving between unconnected patches through time may be better explained by life history attributes than by increasing habitat quality.

Movement distances.– Other studies have also found that corridors do not influence movement distances of small mammals. Bowne et al. (1999) found insignificant differences in the mean net distance moved for cotton rats released into connected and isolated patches at this study site. Cotton rats released into connected patches moved 226 ± 53 m, while those released into isolated patches moved 194 ± 58 m. Mean distances moved in this study are slightly higher; this difference may be accounted for by the different methods used to calculate distance moved. Bowne et al. (1999) calculated the net distance from the release site to the final known location, while we calculated the distance between the 2 farthest points of capture. Bjørnstad et al. (1998) also found that dispersal distances of root voles (*M. oeconomus*) were not affected by corridors.

Results of this study suggest that corridors do not always provide additional connectivity or increase interpatch movement if the species is able to move through the habitat matrix. This ability to move between isolated patches may be due to the distance between patches (128 m), which is small relative to the maximum distances moved by these small mammals. Our results indicate that all 3 species are capable of moving much longer distances. Studies conducted on even larger fragmented landscapes may be necessary to yield more realistic data on the effects of corridors on movement patterns of small mammals.

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CONCLUSIONS

Patch connectivity and habitat enrichment had no significant effect on population densities of cotton rats (*Sigmodon hispidus*), cotton mice (*Peromyscus gossypinus*), or old-field mice (*P. polionotus*). However, connected patches typically had higher densities of cotton rats, while isolated patches had higher densities of old-field mice. Cotton mice were more abundant in connected patches during 1998 and 2000 and in isolated patches during 1997 and 1999. Cotton rats were captured more often than expected in landscape corridors, while cotton mice and old-field mice were captured more often than expected in patch interiors. Home ranges of cotton mice frequently included a high proportion of matrix habitat, and the cotton mouse was the only species captured within the forest matrix, indicating that this species, a habitat generalist, does use the matrix to a greater extent than either the cotton rat or old-field mouse.

Corridors had no effect on home range size of any species; home ranges of animals utilizing connected patches were no larger than those of animals utilizing isolated patches. However, the home ranges of animals that used multiple patch types were significantly larger than those of animals using only a single patch type. Cotton mice and old-field mice were more likely to leave connected than isolated patches; insufficient captures of cotton rats precluded analysis. Relatively high proportions of each species moved between patches that were unconnected to each other, indicating that in this particular fragmented landscape, movements of small mammal species were not limited by forest matrix habitat. Average maximum distances moved did not differ among treatments for any species.

Results of this study suggest that corridors do not always provide additional connectivity between patches. We did not observe any significant effects of corridors or habitat enrichment on population densities. Corridors significantly affected emigration rates of small mammals, but did not influence mean distances moved. The effect of landscape fragmentation on a small mammal species may be highly influenced by the by the quality of matrix habitat, and by the species' response to matrix habitat. Studies conducted at an even larger scale may be necessary to yield greater understanding into the effects of corridors, habitat enrichment, and matrix habitat on population densities and movement patterns of small mammals.