DISSERTATION

DETERMINANTS OF HABITAT USE AND COMMUNITY STRUCTURE OF RODENTS IN NORTHERN SHORTGRASS STEPPE

Submitted by

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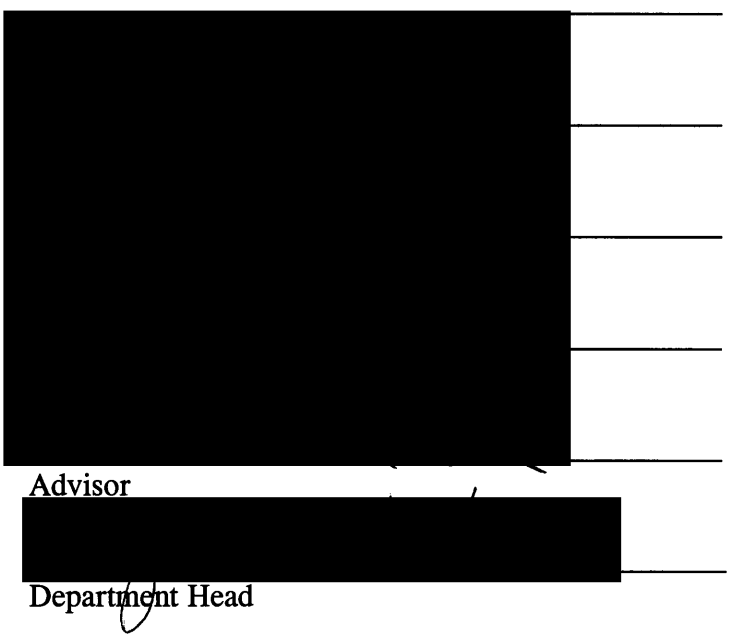
WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY PAUL T. STAPP ENTITLED DETERMINANTS OF HABITAT USE AND COMMUNITY STRUCTURE OF RODENTS IN NORTHERN SHORTGRASS STEPPE BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work



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ABSTRACT OF DISSERTATION

DETERMINANTS OF HABITAT USE AND COMMUNITY STRUCTURE OF RODENTS IN NORTHERN SHORTGRASS STEPPE

Patterns of distribution and abundance of small mammals reflect the responses of individuals to the spatial and temporal availability of resources and abiotic conditions, as well as interactions with conspecifics and other species. I examined habitat selection of two rodents, the deer mouse (*Peromyscus maniculatus*) and the northern grasshopper mouse (*Onychomys leucogaster*), on shortgrass steppe in north-central Colorado. Both species consume arthropods when these resources are plentiful, but grasshopper mice prey on other rodents and thus may have both competitive and predatory effects on deer mice. To examine these interactions, I conducted a removal experiment to determine the effect of grasshopper mice on microhabitat use, diet, and abundance of deer mice, and an odor-response experiment to determine whether olfactory cues mediate interactions between these species.

Deer mice preferred shrubs at both individual and population levels, presumably to reduce predation risk. Mice oriented movements toward shrubs and traveled under shrubs more often than expected based on the density of shrubs on study plots. Population density also increased with increasing shrub density and aggregation. The response of mice to shrub cover was non-linear. Thresholds in the selective use of shrubs, movement patterns, and abundance occurred over a narrow range of shrub cover where shrubs were most aggregated, underscoring the importance of both shrub density and dispersion. Mice tended to accumulate in areas where their movements were most tortuous, suggesting that it is possible to generate testable predictions about patterns of abundance from individual movements.

In contrast, grasshopper mice showed no affinity for shrub microhabitats, and instead oriented movements towards rodent burrows and disturbances created by pocket gophers (*Thomomys talpoides*). Results from pitfall trapping in different microhabitat types suggested that grasshopper mice used gopher mounds and burrows because of the concentration of insect prey in these microhabitats. The abundance of these microhabitats also was a better predictor of grasshopper-mouse abundance than were broad-scale, qualitative descriptors of macrohabitat type. The significance of these microhabitats across scales demonstrates the importance of spatial and temporal availability of prey to grasshopper mice.

Even though grasshopper mice and deer mice show different habitat affinities, grasshopper mice may affect the surface activity and abundance of deer mice in areas where they co-occur. Deer mice decreased in number throughout the removal experiment on both control and removal sites, but the decline was greatest on controls, where grasshopper-mouse numbers increased. No shifts in microhabitat use were detected on removal sites, but deer mice increased their use of shrubs on control sites when grasshopper mice were most abundant. Because diets of deer mice did not differ between control and removal sites during the experiment, grasshopper mice apparently influenced the behavior and populations of deer mice through predation or interference rather than resource competition. Increases in the abundance of granivorous rodents on removal sites support this conclusion, and suggest that grasshopper mice, when abundant, can impact the composition of local assemblages on shortgrass steppe. However, if deer mice actively avoid contact with grasshopper mice, it is unlikely that this interaction is mediated by olfactory cues. When presented with odors of grasshopper mice, harvest mice, and clean cotton, deer mice showed no avoidance of grasshopper-mouse odors, regardless of season, sex or reproductive condition of respondents, or history of contact with grasshopper mice.

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II. RESPONSE OF DEER MICE (*PEROMYSCUS MANICULATUS*) TO SHRUBS: LINKING SMALL-SCALE MOVEMENTS AND THE SPATIAL DISTRIBUTION OF INDIVIDUALS

CHAPTER 1

OVERVIEW AND SUMMARY

Framework, questions, and approach

Patterns of distribution and abundance of animal populations reflect the success of individuals at finding mates, locating sufficient food and nutritional resources, and avoiding predators (Andrewartha and Birch 1954). The consequences of these activities are ultimately manifested in patterns of habitat use, which vary across a range of scales of measurement. At fine spatiotemporal scales, behavioral ecologists have been successful at documenting the decisions made by individual foragers in choosing microhabitats (Stephens and Krebs 1986). Elucidating the mechanisms underlying habitat selection at the population or macrohabitat scale is more complicated, for several reasons. First, the extent of spatial heterogeneity may exceed the dispersal capabilities of most individuals, so that access is restricted to all but subset of possible habitat types. Additionally, site-tenacious individuals that remain in an area regardless of current resource conditions may bias assessments of limiting factors (Wiens 1989). Finally, agonistic interactions between conspecifics may intensify with increasing density, so that subordinate individuals accumulate in poorer-quality habitats (Van Horne 1982, Pulliam 1988). These complications disconnect resource abundance from population size and space use, and limit our ability to use local population density to assess the relative quality of habitats reliably (Van Horne 1983). Yet, because of the relative ease of censusing populations, most tests of habitat-selection theory of free-ranging vertebrates have studied how individuals are distributed among habitats (Fretwell and Lucas 1970) and have not explicitly addressed habitat selection at both behavioral and population scales.

Understanding habitat selection is important to studies of vertebrate communities because habitat partitioning may determine coexistence of similar species and, as a consequence, community organization (Rose and Birney 1985, Kotler and Brown 1988, Kaufman and Kaufman 1989, Brown and Harney 1993). Investigations of the determinants of the structure of small mammal communities conducted during the 1970s and early 1980s emphasized the role of interspecific competition (Dueser et al. 1989). More recently, researchers have emphasized that patterns of microhabitat use reveal differences among species in their vulnerability to predators, so that patterns of distribution and abundance in local rodent assemblages reflect trade-offs between competitive abilities and predation risk (Kotler 1984, Sih et al. 1985, Kotler et al. 1994, Batzli and Lesieutre 1995). However, identifying the mechanisms that determine the structure of rodent communities ultimately requires an understanding of interactions among individuals to complement patterns derived from broad-scale studies of abundance.

My research examined habitat selection of two nocturnal rodents and how resource distributions and interspecific interactions between these species influence patterns of distribution and abundance in semi-arid grasslands of central North America. The studies described here address two general questions:

(1) How do individuals respond to spatiotemporal variation in resource availability and habitat characteristics, and how are these processes translated into patterns of distribution and abundance?

(2) Given that species have different habitat affinities and requirements, what is the role of interspecific interactions in determining the structure of local assemblages, what is the nature of these relationships, and how are they mediated?

My approach was to identify potentially important resources for each species, using existing knowledge from the literature and preliminary studies, and document the response of individuals to spatial and temporal variability in these resources. I used information gained from studies of the behavior of individuals to interpret patterns of habitat use measured at

population scales. With this knowledge, I conducted field experiments to examine how interactions between these species might contribute to patterns of local abundance, and to explore a possible behavioral mechanism through which these interactions might be mediated.

Study area and organisms

The study area was the Central Plains Experimental Range, a region of shortgrass steppe located approximately 60 km northeast of Fort Collins, Colorado. The Central Plains Experimental Range is managed by the United States Department of Agriculture (USDA) Agricultural Research Service and is the location of both the United States International Biological Program (US/IBP) Grassland Biome project (1968-1976) and the National Science Foundation Shortgrass Steppe Long-Term Ecological Research project (1982-present). Detailed descriptions of the vegetation, topography, and climate are provided in the following chapters, and Appendix 1 contains a list of the mammals species found on and adjacent to the USDA Forest Service Pawnee National Grasslands. However, a general description of shortgrass steppe is appropriate here to understand the context within which my field studies were conducted.

Shortgrass steppe is dominated by blue grama (*Bouteloua gracilis*), which forms a largely continuous mat of short perennial grass, interspersed with patches of bare soil, plains prickly-pear (*Opuntia polycantha*) and several species of small shrubs (*Artemisia frigida*, *Gutierrezia sarothrae*, *Eriogonum effusum*). These grasslands are relatively tolerant of grazing by cattle and resistant to invasion from native and exotic plants in the absence of significant disturbances to the soil (Lauenroth and Milchunas 1991). In general, the vegetation has little vertical structure, but at a broader scale, shortgrass steppe is best viewed as a mosaic of grassland and shrubland, with riparian vegetation along permanent streams. The lack of significant cover, coupled with the harsh abiotic conditions common at this location (40° 49' N, 107° 47' W), has presumably led many species to concentrate activity near shrubs and in association with subterranean refuges.

The dominant large shrub on the Central Plains Experimental Range is four-wing saltbush (*Atriplex canescens*), with small soapweed (*Yucca glauca*) present on ridges and sandy soils. Saltbush is primarily restricted to areas in and adjacent to seasonal drainages or low-lying swales, and reaches highest densities in the floodplain of Owl and Cow Creeks, where soils are loam and grasses are mostly blue grama or western wheatgrass (*Pascopyron smithii*). On the more coarsely-textured soils paralleling washes, saltbush and other small shrubs occur with a mixture of both short and intermediate-height grasses.

The diversity and abundance of small mammals is greater on areas where saltbush is present, and in areas of mixed shrub grassland than on open prairie (Chapter 6). Small-mammal studies conducted during the IBP Grassland Biome project focused exclusively on grassland areas and reports from these studies emphasized the low diversity and low population densities of shortgrass prairie compared to other North American grasslands (Grant and Birney 1979, French et al. 1976). Perhaps as a result of these findings, there have been relatively few investigations of the ecology of mammal populations on shortgrass steppe. However, my research, and the preliminary results of long-term monitoring I implemented through the Shortgrass Steppe Long-Term Ecological Research project (Chapter 6, Appendix 1), suggest that a broader view of shortgrass steppe as a landscape mosaic may lead to greater appreciation for the diversity and roles of the native mammalian fauna.

My studies focused on the two most common species of nocturnal rodents (Muridae; Sigmodontinae) on the Central Plains Experimental Range. The deer mouse (*Peromyscus maniculatus*) is ubiquitous, inhabiting both pristine and human-dominated ecosystems throughout most of North America (Hall 1981). This small mouse (20 g) is regarded as a generalist in both diet and habitat (Baker 1968, O'Farrell 1980), although many studies conducted in open-canopy landscapes have demonstrated an affinity for microhabitats with vertical cover (e.g., Holbrook 1979, Thompson 1982, Travers et al. 1988). The affinity of deer mice for shrub microhabitats has often been interpreted as a mechanism for reducing predation risk, as deer mice are common prey for many avian and mammalian predators

(Clarke 1983, Kotler 1985, Marti et al. 1993). Predator populations on my study area are relatively low (Leslie 1992, P. Stapp, pers. obs.) but deer mice may still prefer shrub cover to minimize perceived risk. Because deer mice are often the most abundant small mammal species where they occur, they have frequently been the focal species for experimental studies of rodent communities (Dueser et al. 1989, Kaufman and Kaufman 1989). Studies of interspecific competition have demonstrated that deer mice are often subordinate to specialized rodent species (Dueser and Hallett 1980, Hallett et al. 1983), but that they quickly colonize areas where competitors are removed (Grant 1971, Redfield et al. 1977, Abramsky et al. 1979, Holbrook 1979, Munger and Brown 1981, Brown and Munger 1985).

Grasshopper mice (genus *Onychomys*) are the only insectivorous rodents in North America, and the largest (30 g) of three species, the northern grasshopper mouse, *O. leucogaster*, is the most widespread nocturnal rodent on the Central Plains Experimental Range (Chapter 6). Northern grasshopper mice occur throughout semi-arid and desert grasslands and shrublands from south-central Canada to northern Mexico (Hall 1981) but rarely attain high densities, presumably because their carnivorous habits require large, non-overlapping home ranges (McCarty 1978). Despite the widespread distribution of this species, information on habitat use is limited to broad associations with general vegetation or soil types (e.g. Maxwell and Brown 1968, Kaufman and Fleharty 1974) and virtually nothing is known of its microhabitat affinities. Because grasshopper mice may prey on other rodents (McCarty 1978), understanding the role of grasshopper mice may be useful in interpreting the relative importance of competitive and predatory interactions in the rodent communities.

In the following chapters, I describe the results of 4 yr of field studies to address the questions listed above. Chapters 2 and 3 describe autecological studies of deer mice and grasshopper mice, respectively, and Chapters 4 and 5 describe the results of experimental investigations of interactions between the species. In Chapter 6, I outline the methodology for long-term monitoring studies to track populations of rodents and lagomorphs on the Central Plains Experimental Range and describe the first year of results from this research.

Habitat selection of *Peromyscus maniculatus* and *Onychomys leucogaster*

Researchers have investigated habitat selection using both theoretical and empirical approaches and small mammals have served as useful model organisms. Habitat-selection theories are based largely on the concept of the ideal free distribution (IFD; Fretwell and Lucas 1970), which predicts that individuals distribute themselves among patches of differing quality according to the expected net gain in resources (and hence, fitness) and intraspecific densities relative to other patches. There has been considerable debate about the value of IFD in experimental studies of animal behavior (Kennedy and Gray 1993, Milinski 1994), but IFD is the foundation of the two prevailing models used to describe habitat selection of free-living small mammals (isodar analysis, Morris 1987a; distribution method, Abramsky et al. 1985, Rosenzweig 1985). Because of the logistical difficulties in measuring habitat use of small secretive animals, habitat selection is assessed indirectly in both approaches by comparing patterns of local abundance among qualitatively distinct habitat patches. The emphasis on depletable resources has permitted the extension of these models from single to multiple species using similar resources because intra- and interspecific competition can be estimated in a similar fashion (Rosenzweig and Abramsky 1986, Abramsky et al. 1991). Rosenzweig and Abramsky and their colleagues have used this approach to study interactions among granivorous rodents (e.g. Abramsky and Pinshow 1989, Ziv et al. 1995) and to generate new theories of how density-dependent habitat selection influences community structure.

My studies of habitat use of deer mice and grasshopper mice, in contrast, were largely empirical, in part because the relatively low rodent densities on shortgrass steppe precluded extensive population studies in favor of detailed investigations of microhabitat use. As in earlier field studies of habitat selection by rodents (e.g. Dueser and Shugart 1978, Van Horne 1982, Seagle 1985), I also employed multivariate analyses to quantify habitat characteristics and determine how habitat selection changes with scale. However, where previous studies have usually inferred microhabitat affinities by recording characteristics at capture locations, I obtained information on movements and microhabitat use using fluorescent powder tracking

(Lemen and Freeman 1985). This technique provides a spatial record of an individual's movements without the bias associated with attraction to bait and trapping-area configuration.

In Chapter 2, I demonstrate that deer mice respond to both the overall density and the spatial distribution of shrubs on shortgrass steppe. Patterns of microhabitat use and movement patterns suggested that mice modified their behavior toward shrubs as shrubs became more dense and aggregated. I detected a similar non-linear trend in mouse abundance with increasing shrub canopy cover. I speculate that individual deer mice apparently prefer shrubs to reduce perceived predation risk, although shrubs may also concentrate food resources. At a broader scale, the relationship between abundance and shrub cover may also reflect the scarcity of suitable burrow substrates for deer mice on shortgrass steppe.

In contrast, grasshopper mice showed no affinity for shrub microhabitats and were consistently present in most prairie habitats (Chapter 3). Grasshopper mice instead oriented movements toward rodent burrows and disturbances created by pocket gophers (*Thomomys talpoides*). Comparison between results from pitfall trapping in different microhabitat types and taxonomic composition of arthropod prey in grasshopper-mouse diets suggested that mice used gopher mounds and burrows because of the higher concentration and availability of insect prey in these microhabitats. Variation in the population density of grasshopper mice was best explained by the abundance of these microhabitats rather than broad-scale, qualitative descriptors of soil or shrub cover type.

This result differs from that of Morris (1987b), who found that variation between macrohabitats was a better predictor of the abundance of temperate grassland and forest rodents than microhabitats. One explanation for these differences is that certain resources (e.g., grass, hard mast) differ from mobile insect prey in terms of renewal rates and spatial and temporal predictability. Results from my studies of shrub use by deer mice support this interpretation. I incorporated the microhabitat and macrohabitat variables that were used to study habitat scaling of grasshopper mice (Chapter 3) in a stepwise multiple regression on spatial distribution of deer mice among habitat types. This analysis revealed that deer-mouse

density was best explained by variation at the macrohabitat scale alone ($F=26.31$, $P=0.0001$, $R^2=0.45$) and is consistent with the results of Morris (1987b) for deer mice in other temperate systems. Compared to insects, shrubs therefore may represent a non-depletable resource (i.e., refuge from predation), to which deer mice respond in a relatively fine-grained fashion.

Although movements of deer mice were directed toward shrubs and grasshopper mice oriented movements toward mounds and burrows, the movement patterns of individuals of these species were similar in the shrub-grassland study area where both were tracked (Table 1.1). However, as I note in Chapter 3, densities of large shrubs were approximately two-fold higher than those of mounds and burrows. If movements of both species reflected the density of resources alone, then movement indices should differ between the species. How can we reconcile these discrepancies? I used Eberhardt's index to quantify the dispersion of shrubs, soil disturbances, and burrows. Despite differences in the overall density of these microhabitats, the spatial patterning was not different [means (SE) for Eberhardt's index for dispersion of shrubs, disturbances, and burrows were 1.41 (0.04), 1.50 (0.06), and 1.34 (0.05), respectively, for 16 random transects). Thus, one explanation for similarities in movement may be that individual movements reflect the spatial dispersion of resources as well as overall density (Chapter 2).

Effects of *Onychomys leucogaster* on *Peromyscus maniculatus* and other rodents

Studies of small mammals have contributed much to our understanding of the role of interspecific competition in natural communities (Dueser et al. 1989). Over the past decade, however, researchers have recognized that predators also influence population and community dynamics by selectively removing certain taxa or age and sex classes, or by modifying prey behavior (Longland and Jenkins 1987, Brown et al. 1988, Dickman et al. 1991, Dickman 1992, Lima and Dill 1990). The effects of competition and predation traditionally have been considered separately, but in many ecological systems, one or more species may act as both a competitor and predator with species at similar trophic levels. This phenomenon, termed intraguild predation, has been documented in a number of invertebrate

communities and may be widespread in assemblages of carnivorous and omnivorous vertebrates as well (Polis et al. 1989). The potential impact of predation by grasshopper mice on deer mice and other small rodents, combined with possible dietary overlap between deer mice and grasshopper mice, was the basis for field experiments of interactions between these species on shortgrass steppe. Furthermore, because of the importance of olfactory communication in interspecific interactions of rodents (Drickamer et al. 1992), especially predator avoidance, I tested the hypothesis that deer mice would avoid odors of grasshopper mice to minimize exposure to this potential predator.

I compared patterns of abundance, microhabitat use, and diet of deer mice on four grasshopper-mouse removal sites to those on untreated controls (Chapter 4). Deer mice decreased in number throughout the study on both types of sites, but the decline was greatest on controls, where grasshopper-mouse numbers increased. I detected no microhabitat shifts on removal sites, but deer mice increased their use of shrubs on controls when grasshopper mice became abundant. Because deer-mouse diets did not differ between control and removal sites during the experiment and because mice increased their use of microhabitats typically not used by grasshopper mice, I concluded that grasshopper mice affected deer mice through predation or interference rather than resource competition. Increases in the numbers of granivorous rodents on removals support this conclusion, and suggest that, when abundant, grasshopper mice may impact the structure of local rodent assemblages.

A major criticism of field experiments in community ecology has been the lack of implementation of rigorous study designs that permit accurate conclusions (Hurlbert 1984, Galindo and Krebs 1986, Dueser et al. 1989). Although my experiment was relatively short in duration (3 months), overall I employed a higher level of replication, larger plot sizes, and more frequent monitoring and maintenance of removal effects than previous small-mammal studies (Dueser et al. 1989). Despite of these efforts, natural fluctuations in the deer-mouse abundance confounded my results. However, the area-wide decline in deer mice also led me to speculate that the relative importance of interspecific interactions between deer mice and

grasshopper mice may vary depending on background levels of resource abundance and other external factors that determine successful reproduction of deer mice on a broader scale. For example, in areas of co-occurrence, predation by grasshopper mice during normal years may be opportunistic and focused primarily on juveniles or litters, especially given the affinity of grasshopper mice for rodent burrows. During years of normal or high reproduction, animals lost to predators may be replaced by recruitment from surrounding areas. My experimental plots were intentionally established adjacent to floodplain vegetation, where deer mice consistently reached higher densities, had a more-even sex ratio, a higher proportion of the population reproductive, earlier and more consistent production of juveniles, higher apparent survival rates, and smaller home ranges than in areas of mixed shrub-grassland (P. Stapp, unpublished data). I therefore might not have detected a numerical response of deer mice to changes in grasshopper-mouse numbers had I conducted my study when deer mice were abundant. Furthermore, a decrease in the abundance of insects that reduced food availability for grasshopper mice may cause grasshopper mice to seek rodent prey more actively. For example, predation on other rodents may occur more frequently during winter, when arthropods are less abundant. These results underscore the importance of studying resource availability and the behavior of individuals to understand the mechanisms underlying community patterns.

Although my removal experiment suggests that grasshopper mice affect deer mice in areas where they co-occur, my odor-response experiment provided no evidence that this relationship is mediated by olfactory cues (Chapter 5). When presented with odors of grasshopper mice, harvest mice, and clean cotton, deer mice showed no avoidance of grasshopper-mouse odors. This result was somewhat surprising from previous research demonstrating that rodents generally avoid predator odors, but a detailed review of the studies of odor response of *Peromyscus* species revealed little evidence that these mice respond to heterospecific odors.

Insights and unanswered questions

Taken with earlier small-mammal studies conducted on the Central Plains Experimental Range, my results provide some general insights into what shapes rodent communities of shortgrass steppe (Fig. 1.1). For species such as deer mice, western harvest mice (*Reithrodontomy megalotis*), and also prairie voles (*Microtus ochrogaster*), local abundance is probably determined largely by the abundance of vegetation cover, which provides both food and protection from predators. Granivorous rodents such as kangaroo rats (*Dipodomys ordii*) and locally-rare pocket mice (*Chaetodipus hispidus*, *Perognathus* spp.) respond primarily to soil type through its effect on the production and availability of palatable seeds of annual forbs and intermediate-height grasses. The distribution of grasshopper mice also reflects edaphic conditions, but apparently via the effects of soil friability on other, fossorial rodents and on the consequences of these animals' activities on the availability of arthropod prey. In areas of shortgrass steppe where habitat conditions permit coexistence, grasshopper mice may modify the behavior and population dynamics of deer mice and other rodents. However, the role of an opportunistic predator such as the grasshopper mouse, and of other species interactions, ultimately must be interpreted in the context of overall resource availability, which likely varies with fluctuations in abiotic conditions and the resulting effects on productivity. Human activities such as intensive cattle-grazing and plowing that reduce the structure and diversity of vegetation may have direct effects on species that require seeds or cover, but may also improve conditions for grasshopper mice and hence, influence community structure indirectly.

My findings suggest at least three questions that merit further exploration. First, how general are the apparent non-linear relationships between resource distributions, habitat use, and abundance described for deer mice in Chapter 2? These patterns suggest that our assessment of the importance of habitat features may differ depending on the circumstances (e.g., resource abundance, population density) under which habitat selection is measured, which may complicate elucidation of wildlife-habitat relationships and, as a consequence,

conservation and management efforts. Second, to what degree can differences in patterns of habitat use between organisms at different trophic levels be explained by intrinsic differences in the spatial and temporal predictability and renewal rates of their critical resources? In the context of other studies of habitat selection, my studies suggest that there may be basic differences in scaling of habitat use between granivorous, herbivorous, and carnivorous rodents that reflect differences in the distribution and availability of resources. Finally, traditional studies of predator-prey relationships are often concerned with how predators impact prey populations through direct mortality, but the interactions between omnivorous and carnivorous species may depend indirectly on the abundance of non-shared resources. What are the ecological effects of opportunistic predation and under what conditions can they affect the evolution of local assemblages?

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Table 1.1 Movement indices of powder trails from deer mice tracked during December 1992 and August 1993, and grasshopper mice tracked during January and July 1994 on the shrub-grassland trapping area. Values are means for n paths, with standard errors in parentheses.

	n	Mean vector length	Fractal dimension
Deer mouse	8	0.83 (0.03)	1.16 (0.03)
Grasshopper mouse	12	0.79 (0.01)	1.17 (0.02)

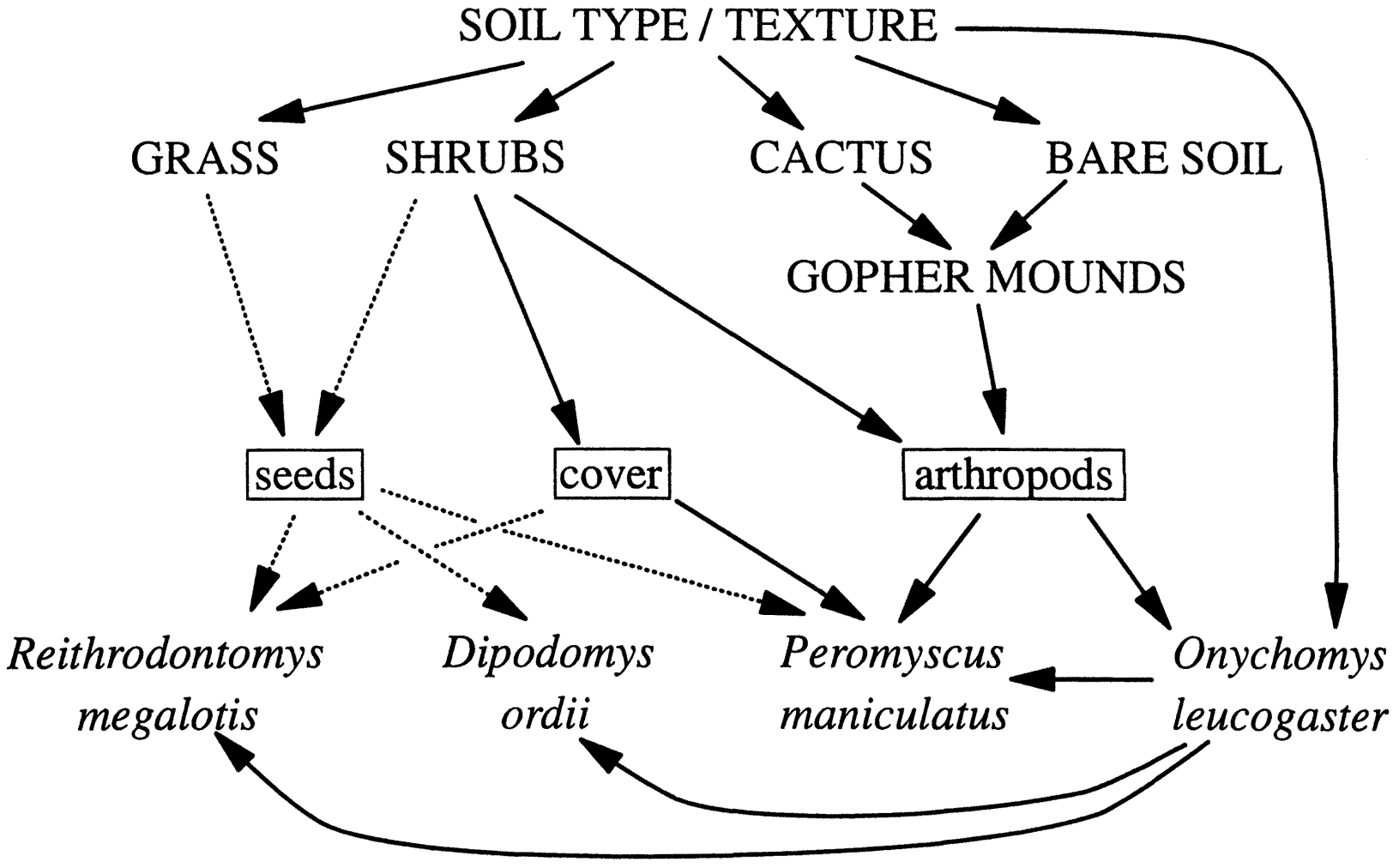

Fig. 1.1. Flow diagram depicting ecological relationships among habitat characteristics (capitalized), resources (in boxes), and the four most common nocturnal rodents (italics) in shortgrass steppe. Interactions represented by stippled arrows were not investigated directly during my research.

CHAPTER 2

RESPONSE OF DEER MICE (*PEROMYSCUS MANICULATUS*) TO SHRUBS: LINKING SMALL-SCALE MOVEMENTS AND THE SPATIAL DISTRIBUTION OF INDIVIDUALS

ABSTRACT

The distribution of individuals and populations may reflect the abundance and spatial distribution of resources across a range of scales but there have been relatively few attempts to link insights from studies of these different phenomena, especially for wide-ranging vertebrates. I live-trapped and tracked deer mice (*Peromyscus maniculatus*) across a gradient of shrub cover on shortgrass steppe in north-central Colorado to estimate population size and quantify patterns of movement and microhabitat use. Mice appeared to prefer shrub microhabitats, especially in areas where shrubs were less numerous, and to orient their movements toward shrubs and shrub patches. Population density also increased with increasing density and aggregation of shrubs. Furthermore, thresholds in the selective versus random use of shrub microhabitats, movement patterns, and population density occurred over a narrow range of shrub cover where shrubs were most aggregated, underscoring the importance of both the density and dispersion of shrubs. Relationships between shrub cover and movement parameters and abundance suggested that mice accumulated in areas where their movements were most tortuous. Information on movements of individuals therefore can produce testable predictions about patterns of local abundance and may provide insights into the relationship between space use and population size.

INTRODUCTION

Ecologists have generally approached the study of natural populations from two directions (Hassell and May 1985). Behavioral ecologists typically seek adaptive explanations for the responses of individuals to resources, conspecifics and predators, with the objective of discerning how these behaviors ultimately contribute to survival and reproductive success. Population ecologists, on the other hand, are concerned primarily with demographic processes such as mortality, fecundity and dispersal, and the consequences of these factors for the distribution and abundance of individuals. Behavioral and population phenomena are usually addressed at different spatial and temporal scales, but the study of animal movement is central to both approaches (Stenseth and Lidicker 1991). Indeed, several authors (e.g. Crist and Wiens 1995, Wiens et al. 1993, Johnson et al. 1992, Turchin 1991) have argued that the spatial structure of populations emerges from the collective behavior of individuals interacting with landscape features, and that knowledge of the mechanisms underlying the movements of individuals will improve our understanding of patterns of spatial distribution and abundance.

Researchers have attempted to link individual behavior and population phenomena using a variety of theoretical approaches, including models based on game theory (e.g. Goss-Custard et al. 1995), differential equations of predator-prey and population dynamics (Kareiva and Odell 1987, Hassell and May 1985), individual-based movements (reviewed by Johnson et al. 1992), and diffusion or random walks (e.g. Crist and Wiens 1995, Gautestad and Mysterud 1993, Benhamou and Bovet 1989). Turchin (1991) reviewed diffusion and random-walk approaches and proposed a mathematical model to calculate the spatial distribution of foragers from empirically-derived parameters of individual movements. Wiens and his co-workers (Crist and Wiens 1995, Wiens et al. 1995, Crist et al. 1992, Johnson et al. 1992, Wiens and Milne 1989) have advocated the use of experimental model systems, in which one records the behavior of small organisms, usually insects, in artificial or manipulated "microlandscapes". The goal of this approach is to extrapolate pattern-process

relationships from rigorous, small-scale experiments to ecological systems at broader scales. These efforts have contributed to our understanding of the mechanistic basis of animal movement, but applications of these insights to natural systems involving wide-ranging vertebrate organisms have remained elusive.

In this paper, I describe how patterns of abundance of a small mammal reflect responses to the spatial distribution of habitat components that are similar to those observed in movements of individuals within their home ranges. I recorded the nocturnal movements of deer mice [*Peromyscus maniculatus nebracensis* (Coues)] with respect to woody shrubs, and compared patterns of abundance to the distribution of shrub cover on shortgrass steppe, an area of semiarid grasslands in the central United States. Shortgrass steppe is dominated by short, perennial grasses and has little vertical structure except in low-lying areas, where soil texture permits establishment of large shrubs (Lauenroth and Milchunas 1991). Small rodents such as deer mice are more abundant in shrub-dominated areas than in open grasslands (Chapter 6; Lindquist et al. 1995), reflecting the importance of vegetative cover for quadrupedal rodents in arid and semiarid regions of North America (Kotler and Brown 1988). Deer mice attain a wide range of densities across gradients of shrub cover on my study area in north-central Colorado, which allowed me to document habitat selection at microhabitat and macrohabitat scales (Rosenzweig 1989).

My study addresses four questions. First, do deer mice prefer shrub microhabitats in shortgrass steppe? Second, how do the movements of individual deer mice reflect their response to shrub cover? Third, what is the relationship between the relative abundance of mice and the abundance and spatial distribution of shrubs? Last, can we predict the spatial distribution of deer mice along gradients of shrub cover from the movement characteristics of individuals?

MATERIALS AND METHODS

My study area was the Central Plains Experimental Range, located ca. 60 km northeast of Fort Collins, Colorado, USA. Research at the 6200-ha site is coordinated by the

USDA Agricultural Research Service and the Shortgrass Steppe Long-Term Ecological Research project (National Science Foundation). The climate is semi-arid: mean monthly temperatures range from -5°C in January to 22°C in July, and ca. 70% of the 321 mm of annual precipitation falls during late spring and summer (Milchunas and Lauenroth 1995). Upland vegetation is short in stature and dominated by two perennial bunchgrasses [*Bouteloua gracilis* (H.B.K.) Lag. and *Buchloe dactyloides* (Nutt.) Engelm.], with a mixture of small shrubs and forbs [*Artemisia frigida* Willd., *Eriogonum effusum* Nutt., *Sphaeralcea coccinea* (Pursh) Rydb.], and prickly-pear cactus (*Opuntia polycantha* Haw.). Low-lying areas have abundant large shrubs [primarily four-wing saltbush, *Atriplex canescens* (Pursh) Nutt.] and a variety of half-shrubs [*A. frigida*, *E. effusum*, *Gutierrezia sarothrae* (Pursh) Britt.and Rusby, *Ceratoides lanata* (Pursh) J.T. Howell, *Chrysothamnus nauseosus* (Pall.) Britt.] and mid-grasses (*Pascopyron smithii* (Rydb.) A. Löve, *Stipa comata* Trin. and Rupr., *Aristida longiseta* Steud., *Sitanion hystrix* (Nutt.) J.G. Smith, *Oryzopsis hymenoides* (Roem.and Schult.) Ricker]. Small soapweed (*Yucca glauca*) occurs primarily on ridges and on sandy soils. A broad floodplain associated with two ephemeral creeks is on loamy soils with thick grass (*B. gracilis* and *P. smithii*) and dense saltbush. Upland sites are grazed by cattle in summer and fall, whereas shrub areas are mostly grazed in winter and spring.

Gradients in shrub density occur on the study area, with high densities of saltbush on the floodplain, intermediate shrub densities on adjacent coarsely-textured soils, and no large shrubs on upland prairie. I estimated relative densities of deer mice by live-trapping on sites with varying amounts of shrub cover. Mice were trapped on three 1.82-ha rectangular grids in winter 1992/93 (20 December 1992 - 31 January 1993) and summer 1993 (16-28 July), nine 1.54-ha circular webs (Buckland et al. 1993) in early summer 1994 (7-15 June) and 25 0.32-ha rectangular plots in early summer 1995 (27 May - 3 July; Table 2.1). Relative densities were calculated as the number of individuals captured on each site, divided by the effective trapping area. The effective trapping area (Table 2.1) was the area bounded by the traps, plus a 18-m boundary strip to adjust for movement of mice onto the trapping areas.

The width of the boundary strip was one-half the average maximum distance moved between captures of deer mice based on other trapping studies (P. Stapp, unpublished data). I used the mean density from winter and summer 1993 trapping periods for each grid so that each site was only represented once in analyses. Traps were baited with peanut butter and oats and checked at dawn. Trapping was conducted during the dark phase of the lunar cycle (>5 days prior to or after full moon).

To describe the distribution and abundance of shrubs on trapping areas, I estimated shrub density by recording the number of shrubs (≥0.3 m in height) within a 2-m radius of random points (n = 50, 28, and 16 points for grids, webs, and plots, respectively). Shrubs were usually saltbush or soapweed. The distance from each point to the nearest shrub was recorded and used to calculate Eberhardt's index as a measure of shrub dispersion on trapping sites, defined as:

$$\text{Eberhardt's Index} = (CV/100)^2 + 1.0, \qquad (1)$$

where CV is the coefficient of variation of the point-to-shrub distances (Krebs 1989). Values of Eberhardt's index below 1.27 (CV=52%) suggest a regular pattern of shrubs, whereas larger values indicate clumping (Krebs 1989).

Fluorescent powder tracking (Lemen and Freeman 1985) was used to measure surface movements and microhabitat use of deer mice in relation to shrub cover. Deer mice were tracked on the three 1.82-ha grids during winter 1992/93 and summer 1993 and on the nine trapping webs in summer 1994 (Table 2.1). Captured mice were removed from the trapping site and held at the field headquarters in traps. Extra bedding, bait, rodent chow, and a slice of apple or potato were provided to mice. Approximately 1-2 h before sunset, mice were dusted with fluorescent powder (Radiant Color, Inc., Richmond, California) and released at their capture locations. Mice usually escaped to burrows or to the base of shrubs and these locations were flagged. Because mice occasionally changed burrows before nightfall, however, I returned to these locations at dusk and followed the powder to the animal's final daytime location. To ensure that I only recorded nocturnal movements, I used the final

daytime location as the starting point for measuring movements. In all but a few instances, dusted mice were in burrows at dusk; for mice remaining on the surface (always beneath shrubs), tracking began at the first burrow entered. Mice were not dusted and released in the morning after capture because my preliminary studies indicated that daytime grooming by mice often resulted in short, fragmented trails.

Beginning at approximately 4 h after sunset, powder trails were followed using ultraviolet-light flashlights and marked at 1-m intervals with flagged nails. In December 1992 and August 1993, trails were marked from their final daytime location to the first burrow entered (a surface bout). In June 1994, only the first 50 m of powder trails was marked. Distances and turning angles of marked trails were measured and mapped using electronic surveying equipment (Pentax PTS-II05 total station, Tokyo, Japan) connected to a field data-logger (Corvallis Microtechnology MC-II, Oregon, USA). With the exception of one mouse that was tracked in both December 1992 and August 1993, each trail represented a different individual.

I calculated two indices to describe the movement patterns of mice. Mean vector length (Batschelet 1981) is a measure of the directionality of the trail that is based on the distribution of turning angles, and ranges from 0 for meandering trails to 1.0 for linear movement in one direction. Fractal dimension (Mandelbrot 1983) describes the tortuosity of movement trails and takes values from 1.0 for straight movements to 2.0 for convoluted trails that, if infinitely long, would fill a plane (dividers method; Dicke and Burrough 1988, With 1994).

To describe how mice used shrubs, I counted the number of 1-m trail points beneath shrubs and measured the distance from each point to the nearest shrub. Points within 0.1 m of shrubs were considered beneath shrubs. The coefficient of variation of point-to-shrub distances for each trail was used to describe the tendency of mice to concentrate activity near to or far from shrubs. The distance from the nearest shrub to its three nearest neighbors was also measured at one randomly-chosen point from each 5-m segment of trails from August

1993 and June 1994. The mean of these distances provided an index of inter-shrub spacing in the area of the trails.

I compared the percentage of trail points beneath shrubs to the percentage of random points beneath shrubs for each site to determine whether mice used shrubs to a greater degree than expected from the density and dispersion of shrubs on trapping areas. I also calculated Eberhardt's index for trails, using the coefficient of variation of the trail-to-shrub distances from the randomly-chosen points (i.e., each 5-m segment) rather than all trail points. Eberhardt's index was used to determine whether mice oriented movements toward shrubs. If mice concentrated activity either nearer to or farther from shrubs than expected based on shrub dispersion, then trails should have higher coefficients of variation and higher values for Eberhardt's index than the trapping area. I then compared the mean distance from trails to shrubs to the mean distance from random points to shrubs on trapping areas to determine whether mice were relatively close to or far from shrubs. Paired tests (t-tests, Wilcoxon sign-rank tests) were used for both comparisons. I used SAS (SAS Institute 1989) for all statistical analyses.

RESULTS

I tracked 12 and 17 mice on trapping grids in winter 1992/93 and summer 1993, respectively, and 27 mice on trapping webs in summer 1994, for a total of 56 powder trails. Mean trail length was 51.57 m (standard deviation, SD=22.17), with a mean net displacement (straight-line distance) of 31.02 m (SD=18.18). Movement indices were highly correlated (Table 2), but there was no relationship between these parameters and trail length (Spearman $|r_s| \leq 0.03$, $P \geq 0.79$), indicating that movement indices were not biased by differences in the length of trails I marked. The significant correlations between the percentage of trail points under shrubs and movement indices (Table 2.2) indicated that trails beneath shrubs were convoluted, whereas those in the open microhabitats were linear and more directed. Trails that moved in and out of shrubs had high coefficients of variation and, generally, high values of fractal dimension (Fig. 2.1a), suggesting that movements were directed toward shrubs or

shrub clusters. Mean vector length increased with the average distance between shrubs along trails (Fig. 2.1b), so that mice made straighter movements in areas where shrubs were widely spaced. For a given trail, there was no difference between the mean distance to nearest shrub and one-half the average distance between shrubs (Wilcoxon sign-rank test, S=72, P=0.407). Thus, regardless of shrub spacing, mice apparently moved so as to split the distance between shrubs and minimize their travel in shrub inter-spaces.

Deer-mouse numbers were extremely variable among sites and mice were often absent from seemingly suitable habitat. The relative density of mice was positively correlated with shrub density (Fig. 2a; r_s=0.55, P=0.0004), even though the highest and lowest densities occurred on sites with similar densities of shrubs. Population density also increased linearly with the aggregation of shrubs (Fig. 2.2b; r_s=0.39, P=0.016) and mice were most numerous in areas where shrubs were most clustered. The relationship between Eberhardt's index and shrub density on sites was unimodal (second-order polynomial regression, P=0.002, r^2=0.31; shrub density log-transformed to normalize and improve variance); shrubs became more aggregated with increasing density until an estimated shrub density of 0.33 shrubs/m^2 (Eberhardt's index=1.75). The relationship between the density and percent cover of shrubs (arcsine-square root transformed) was linear (P=0.0001, r^2=0.56) and at 0.33 shrubs/m^2, I estimated shrub cover to be 10.63%.

Patterns of shrub use along powder trails indicated that mice used shrub microhabitats differently than expected based on the spatial distribution of shrubs on trapping areas. Eberhardt's index of trails ($\bar{x}$=1.84, SE=0.06) was significantly greater than that of sites ($\bar{x}$=1.70, SE=0.03; paired t-test, t=2.31, P=0.025). Because trails were also closer to shrubs than expected based on random point-to-shrub distances (trail $\bar{x}$=0.87 m, SE=0.08; site $\bar{x}$=2.21 m, SE=0.31; sign-rank test, S=-622, P=0.0001), I concluded that mice directed their movements toward shrubs. In addition, the proportion of the trail points beneath shrubs was greater than that of random site points (t=2.32, P=0.053), indicating that mice preferred shrub microhabitats. Although the percentage of trail points beneath shrubs remained constant

regardless of shrub cover ($\bar{x}$=19.08%, SE=1.49, n=56; r_s=0.29, P=0.363), their affinity for shrubs changed as shrubs became more abundant (Fig. 2.3a). Mice seemed to prefer shrub microhabitats on sites with shrub cover below ca. 11% (t=6.96, P=0.0001, n=10) and the relationship between shrub cover and the selective use of shrubs was relatively constant over this range (r_s=0.02, P=0.945). However, mice showed no affinity for shrubs on the sites with the most shrub cover (t=-1.80, P=0.32, n=2; Fig. 2.3a). In addition, movements of mice became more tortuous and less directional with increasing shrub cover until 11% (fractal dimension, r_s=0.640, P=0.046, Fig. 2.3b; mean vector length, r_s=-0.66, P=0.038), after which movements were similar to those on sites with the fewest shrubs (Fig. 2.3b).

Population densities of mice also increased with increasing shrub cover on trapping areas. Although the relationship was relatively linear overall (r_s=0.68, P=0.0001), density increased with shrub cover at values below 11% (r_s=0.49, P=0.016, n=24), but was more variable and constant above 11% (r_s=0.42, P=0.153, n=13; Fig 2.3c.). Thus, transitions in the selective use of shrub microhabitats, movements, and abundance occurred at approximately the same value of shrub canopy cover (11%), and this threshold was similar to the peak in the relationship between shrub density and shrub dispersion (10.63% cover).

DISCUSSION

My results suggest that shrubs are important resources for deer mice on shortgrass steppe. I have shown that mice preferred shrub microhabitats, especially in areas where shrubs were relatively rare, and that they seemed to orient their movements toward individual shrubs. Furthermore, mice reached highest densities in areas where shrubs were most dense and aggregated. The relationships among shrub cover, movement indices, and population density suggest that mice tended to accumulate in areas where their movements were most tortuous. This result may be somewhat intuitive, but shows that it is possible to predict general patterns of abundance from spatial information on individual movements. Finally, using three independent measures that described microhabitat selection, individual movements, and abundance, my results suggested thresholds in the response of mice to

shrubs at multiple scales. Additional data on movements and microhabitat-use patterns are needed to determine whether these patterns are real and meaningful. However, that these thresholds occurred at approximately the level of shrub cover where shrubs were most aggregated suggests that mice responded at both behavioral and population scales to the abundance and spatial patterning of shrubs.

The data available from powder tracking were purely spatial and therefore provided no information on how long mice spent in particular microhabitats, but my methods nonetheless allowed me to document a number of important aspects of habitat use. For example, the absence of a significant correlation between average shrub spacing and the coefficient of variation of trail-to-shrub distances revealed that these variables described different aspects of the behavioral response to shrubs. Average shrub spacing measured the spatial patterning of shrubs in the areas where mice chose to travel, whereas the coefficient of variation reflected how mice moved in response to individual shrubs. Given that these indices described habitat use at somewhat different scales, it is not surprising that mean vector length, which measured the overall directionality of movement, was correlated with shrub spacing, and that fractal dimension, an index of the amount of turning in trails, was more related to the behavioral response to individual shrubs or shrub clusters (Table 2.2).

Additionally, patterns in the relative proportion of the trail beneath shrubs revealed that the affinity for these microhabitats changed in a non-linear fashion with increasing shrub cover. Mice selected shrub microhabitats where shrubs were relatively uncommon or dispersed, but above some critical level of shrub cover, they were able to remain relatively close to shrubs without entering the shrub canopy. Mice did not change the amount of travel beneath shrubs but instead modified their movement patterns to reflect changes in the distribution of shrub cover. Movement trails were relatively straight at both high and low values of shrub cover, but apparently, for different reasons. Where shrubs were rare, mice moved linearly to minimize travel in the open. Trails were also relatively straight on sites with high shrub canopy cover, but because mice presumably achieved the benefits of

proximity to shrubs without traveling beneath them. Movements reflected changes in the availability of shrubs only over a narrow, intermediate range of shrub cover. Therefore, one's perception of the relative importance of shrubs to mice, as well as the scale at which mice perceive and respond to variation in the distribution of shrubs, might differ depending on the range of shrub cover at which one measured habitat use.

If the short-term movements of individuals provide a relative measure of space use and area requirements (cf. Mullican 1988), then movement patterns and population size in general should be inversely correlated for a given species. The nature of this relationship, however, depends on both the abundance and distribution of resources. In my study, density and movement indices were not correlated (Table 2.2), even though both were affected by the amount of shrub cover present. Population density may reflect individual movements if resources are continuous or if individuals are territorial, but space use is also strongly affected by the spatial configuration of resource patches and their relative quality. Thus, one explanation for the lack of a significant relationship between abundance and movement patterns is that I measured movements over an array of resource distributions but not across a sufficiently broad range of population size. Additionally, I emphasize that my tracking studies were conducted at relatively low population densities (2-4 individuals/ ha). Whereas this presumably allowed me to detect habitat selection with minimal effects of conspecifics (Rosenzweig 1989), for many organisms, habitat use and movements are also determined by intraspecific interactions, which likely become more significant at higher population densities. My observation that population density was more variable on sites with the highest canopy cover of shrubs (Fig. 2.3c), for example, suggests that above some level of resource abundance, population size may be determined by factors other than resources alone. The extent to which one can successfully predict the spatial distribution of individuals and resources using individual movements therefore depends on our understanding of the effects of interactions among conspecifics on local abundance. Correct interpretation of patterns of

habitat selection, for example, requires knowledge of whether low density results from sparse or patchy resources or from despotic effects of dominant individuals.

There are several possible explanations for the apparent affinity of deer mice for shrub microhabitats on shortgrass steppe. First, as many researchers have noted, small quadrupedal rodents such as deer mice may preferentially use shrubs and avoid open spaces to reduce risk of predation (see review by Kotler and Brown 1988). Great horned owls (*Bubo virginianus*) are the primary avian predator of mice on my study area (Zimmerman et al., in press), but owl densities are relatively low because of the rarity of suitable roosting and nesting sites (Leslie 1992). I recently found that deer mice increased their use of shrubs when grasshopper mice (*Onychomys leucogaster* Rhoads) were abundant (Chapter 4). By traveling in shrubs, deer mice therefore may avoid grasshopper mice, which may prey on other rodents (McCarty 1978) and show no affinity for shrub microhabitats (Chapter 3). Regardless of whether predation is an important source of mortality, deer mice may associate openings with perceived risk and hence prefer to travel beneath shrubs.

Alternatively, in open vegetation such as shortgrass steppe, shrubs may represent patches of concentrated food resources by collecting wind-blown seeds or as thermal refuges for insect prey. Deer mice are omnivorous and most of their spring and summer diet consists of arthropods (Chapter 4, Flake 1973). Many insects also prefer shrub microhabitats (P. Stapp, unpublished manuscript) and mice may encounter prey more frequently by using shrubs (Harris 1986). The small-scale distribution of insects cannot explain the microhabitat affinities of mice during winter, but favorable microclimates associated with shrubs also may protect mice from severe weather.

Finally, at a broader scale, the relationship between mouse abundance and shrub cover may also reflect the availability of suitable burrows and nest sites across gradients in vegetative cover and soil type. On my study area, saltbush is restricted to low-lying areas, where soil texture is usually coarse, and deer mice may not be able to excavate burrows in areas where soils are more compacted or where grass cover is continuous. Soils at the base of

shrubs may be more friable and thus more amenable to burrowing (Wiener and Capinera 1980), and mice may be able to use small crevices among the roots of shrubs as refuges or nest sites. Densities of unoccupied burrows are also higher in shrub-dominated areas than in open grasslands because rodents in general tend to be more numerous on saltbush sites (Chapter 6; Lindquist et al. 1995). Although experimental studies may ultimately determine whether shrubs function primarily as refuges from abiotic conditions or predators, or as foraging sites, shrubs probably perform all of these roles.

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Table 2.1. Summary of trapping-area design and methodology. Trapping sessions were periods of consecutive nights during which traps were set in evening and checked at dawn. A single large Sherman trap was placed at each station and baited with a mixture of peanut butter and oats. Individuals were marked with aluminum ear tags (1992-1994) or with permanent felt markers (1995). See text for additional details.

Site type (n)	Trapping dates	Number of nights	Number of traps	Trap spacing	Area (ha)	Effective area (ha)	Number of mice tracked
Grids (3)	Winter 1992-93	5	100 (10X10)	15 m	1.82	2.92	12
	Summer 1993						17
Webs (9)	Summer 1994	4	57 (8 transects, 7 traps each)	10 m	1.54	2.43	27
Plots (25)	Summer 1995	3	32 (4X8)	15 m, 10 m	0.32	0.86	0

Table 2.2. Spearman rank correlation matrix for movement parameters and use of shrubs along powder trails of deer mice. N = 56 trails for all variables except SPACE (N = 44), which was not recorded for the 12 mice tracked in January 1993. The top value in each cell is the Spearman correlation coefficient, with the associated two-tailed probability listed below. MVL, mean vector length; FRACTAL, fractal dimension; CVDIST, coefficient of variation of trail-to-shrub distances (%); PSHRUB, percentage of trail points beneath shrubs (%); SPACE, average inter-shrub spacing along trail (m); DENSITY, population density (individuals/ha) on areas where mice were tracked.

	MVL	FRACTAL	CVDIST	PSHRUB	SPACE
FRACTAL	-0.426	1.0	-	-	-
	0.0006	0.0			
CVDIST	-0.237	0.408	1.0	-	-
	0.079	0.002	0.0		
PSHRUB	-0.388	0.265	0.681	1.0	-
	0.003	0.048	0.0001	0.0	
SPACE	0.460	-0.047	-0.218	-0.663	1.0
	0.002	0.764	0.154	0.0001	0.0
DENSITY	-0.017	-0.036	-0.197	0.058	-0.170
	0.898	0.793	0.145	0.673	0.269

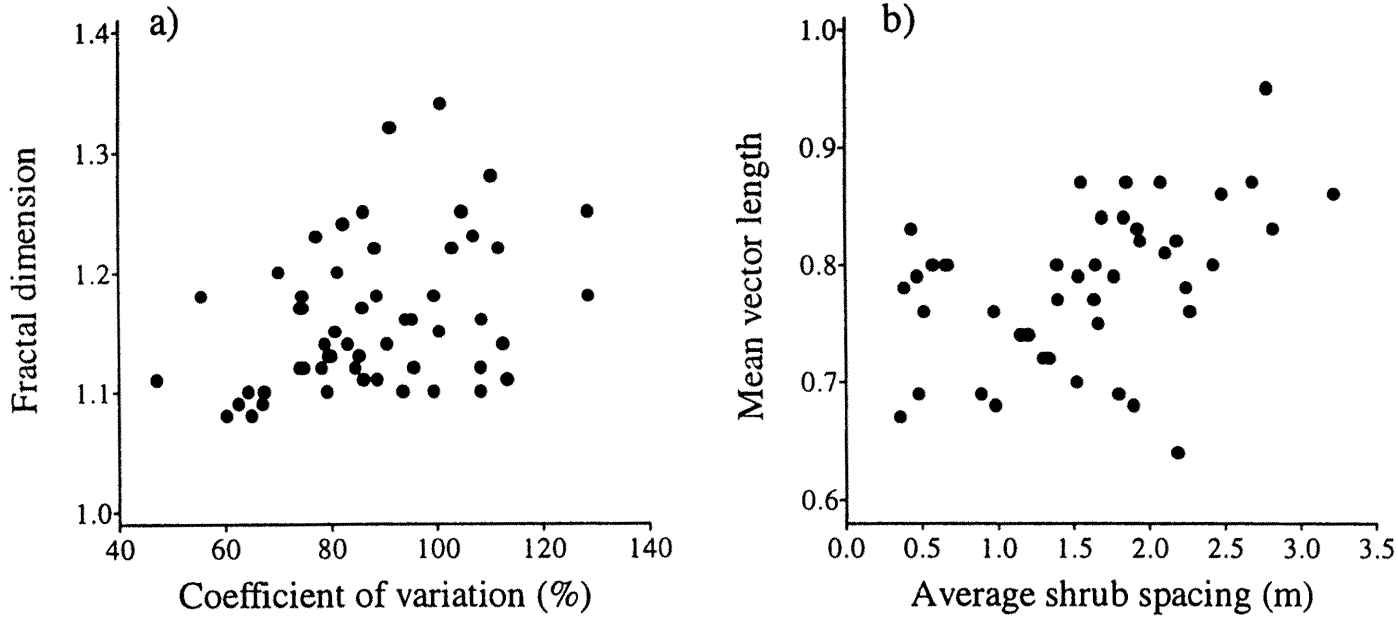

Fig. 2.1. Movement patterns of deer mice (*Peromycus maniculatus*) with respect to shrubs on shortgrass steppe. The coefficient of variation (a) described movement in and out of shrubs, whereas average shrub spacing (b) describes patterns of shrub spacing along trails. See Table 2 for statistical analyses.

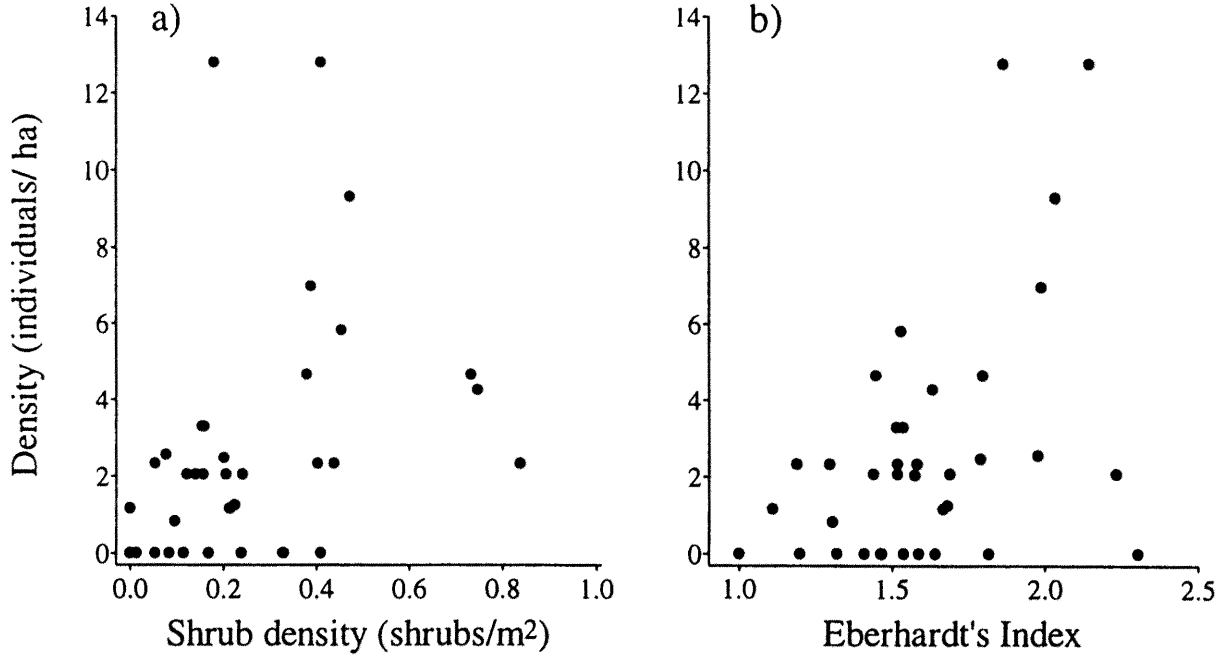

Fig. 2.2. Relative density of deer-mouse populations across a gradient of the density (a) and dispersion (b) of shrubs on 37 trapping areas of shortgrass steppe. Shrub density was log-transformed prior to analysis, but non-transformed values are presented.

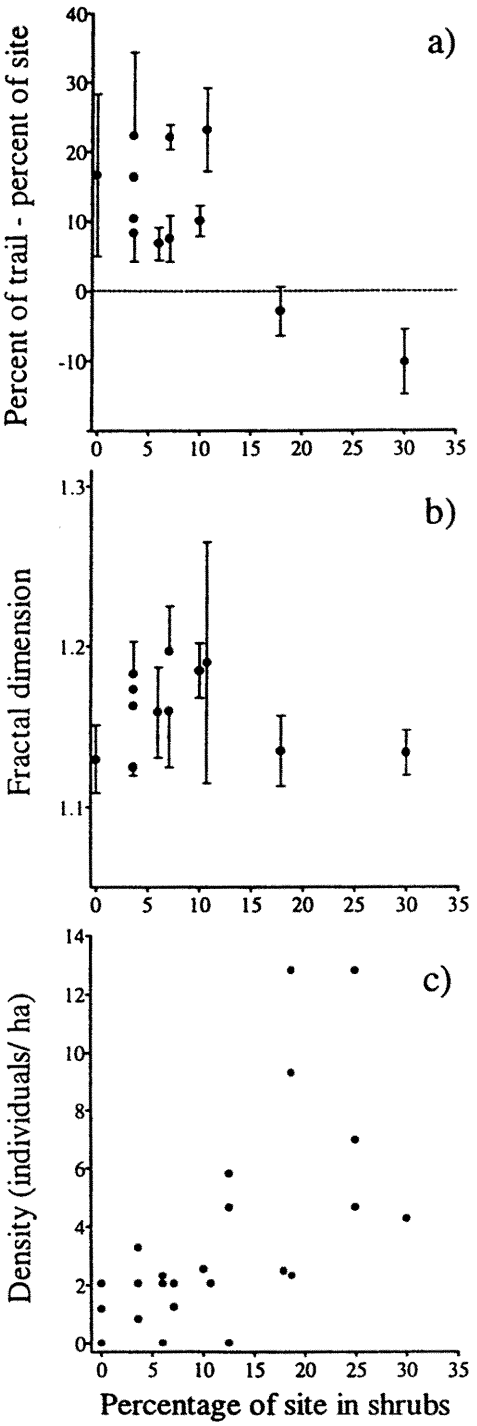

Fig. 2.3. Relative use of shrubs along trails, movement patterns, and abundance of deer mice as a function of the percentage of shrub canopy cover on trapping areas. a) the selective use of shrubs, expressed as the mean (±SE) difference between the percentage of trail points beneath shrubs and percentage of random points beneath shrub for a given site (for clarity, only extreme SE are presented for sites with the same values for shrub cover). Values above the dashed line represent greater use of shrubs than expected from shrub cover on the site; b) tortuosity of movement trails, expressed as the mean (±SE) fractal dimension of trails on each site; c) population density of mice on the 37 trapping areas.

CHAPTER 3

EFFECTS OF VEGETATION AND SUBSTRATE CHARACTERISTICS ON PREY AVAILABILITY AND HABITAT SELECTION OF NORTHERN GRASSHOPPER MICE (*ONYCHOMYS LEUCOGASTER*)

ABSTRACT

Patterns of habitat selection of small mammals reflect responses to variation in resource availability at a range of spatial and temporal scales. I investigated habitat use of northern grasshopper mice (*Onychomys leucogaster*) on shortgrass prairie and related these patterns to the distribution of vegetation and substrate characteristics and the availability of arthropod prey. I used powder tracking to document microhabitat use and live-trapping to estimate abundance on sites with different soil types and amounts of shrub cover (macrohabitats). At all spatial scales examined, mice utilized soil disturbances (primarily *Thomomys talpoides* mounds) and burrows more than expected based on the abundance of these microhabitats, but showed no affinity for large shrubs. Furthermore, movement patterns suggested that mice concentrated activities in areas with high densities of mounds and burrows. Prey were more numerous on gopher mounds than in other microhabitats and were generally more abundant in trapping areas where grasshopper mice were captured, especially in spring and early summer. Mounds and burrows provide arthropods with access to subterranean refuges, and the concentration and accessibility of prey thus may explain the intensive use of these microhabitats. Microhabitat variables associated with disturbances and burrows also were better predictors of population density than was macrohabitat, which likely reflected the aggregated spatial distribution and temporal predictability of insect prey.

Although the local abundance of grasshopper mice was influenced primarily by the distribution of suitable foraging microhabitat, the relationship between these habitat features and substrate characteristics indicates that it may be difficult to separate the roles of microhabitat and macrohabitat for this wide-ranging species.

INTRODUCTION

Habitat selection can be viewed as a process by which the behavioral decisions made by individuals are translated into patterns of distribution and local abundance. For many organisms, this process is hierarchical (Johnson 1980), but it is not clear that information on movements and habitat use collected at fine scales is necessarily useful for predicting population size at broader scales. Ornithologists, for example, have long recognized that birds may use different proximate cues to choose nesting locations within a territory than they use to select territories from the surrounding landscape (e.g., Bergin 1992, Brennan et al. 1987, Hildén 1965, Orians and Wittenberger 1991, Wiens 1985). For less-vagile organisms such as small mammals, the hierarchical nature of habitat selection may be less obvious because these animals may only be able to sample a restricted range of the habitat spectrum. Morris (1987) emphasized that rodents perceive and respond to habitat characteristics at a variety of scales and advocated an organism-centered view of habitat selection. Except for Morris' work (e.g., 1984, 1989, 1992), however, few researchers have attempted to incorporate scaling explicitly in studies of habitat selection of small mammals.

The northern grasshopper mouse (*Onychomys leucogaster*) is a useful model organism for studying how habitat selection varies across temporal and spatial scales and how this variation contributes to patterns of abundance in heterogeneous landscapes. Northern grasshopper mice are widely distributed, occurring from southern Canada to northeastern Mexico (Hall 1981), and are found throughout arid and semi-arid regions of western North America. Individuals may range over several hectares (McCarty 1978) and therefore likely respond to variation in habitat characteristics recognizable at large, macrohabitat scales. Because grasshopper mice also are insectivorous (Bailey and Sperry 1929, Flake 1973),

however, patterns of microhabitat use probably also reflect small-scale spatial variation in the availability of arthropod prey. Temporal variation in the abundance and accessibility of arthropods on both a seasonal and nightly basis may further affect patterns of habitat use, particularly at northern latitudes.

Despite the ubiquity of northern grasshopper mice in western grasslands and shrublands, information on the habitat preferences of this species is mostly restricted to associations with broad classes of vegetation or edaphic conditions (e.g., Egoscue 1960, Kaufman and Fleharty 1974, Maxwell and Brown 1968, Moulton et al. 1981). The lack of detailed information on the ecology of natural populations of grasshopper mice probably is a function of the low population densities at which this species typically occurs (McCarty 1978). However, grasshopper mice are among the most common rodents on shortgrass-prairie regions of the Central Plains (Choate and Terry 1974, Grant et al. 1977).

Population densities of grasshopper mice and other small mammals on shortgrass steppe vary markedly across gradients in vegetation and substrate conditions (Grant et al. 1982, Lindquist et al. 1995). Grasshopper mice avoid litter and dense vegetation and prefer patches of bare ground (Abramsky et al. 1979), and Egoscue (1960) speculated that these mice required loose sandy soils for dust-bathing. Alternatively, grasshopper mice may choose unvegetated areas for ease of travel or because these areas support higher densities of insect prey. For example, terrestrial arthropods may be attracted to disturbances and burrows created by pocket gophers (*Thomomys*, *Geomys* spp.) and kangaroo rats (*Dipodomys* spp.; Hawkins and Nicoletto 1992, Huntly and Inouye 1988). Prey may also be more accessible in these microsites because soils are more friable than adjacent locations.

It is difficult to evaluate the relative merits of these hypotheses without detailed information on habitat use with respect to the distribution of resources. In this paper, I describe seasonal patterns in habitat use of northern grasshopper mice on shortgrass prairie in north-central Colorado, and identify potential mechanisms underlying the selection of habitats across a range of spatial scales. I used powder tracking to quantify movements and habitat

use, and live-trapping to estimate local abundance on areas with differing vegetation and soil conditions. I also conducted pitfall trapping to assess the microhabitat distribution of insect prey and to quantify prey abundance on areas with different grasshopper-mouse densities. Finally, I combined information on prey availability and vegetation and substrate characteristics with a detailed examination of arthropod consumption by grasshopper mice to interpret patterns of habitat use and abundance on shortgrass-prairie habitats.

METHODS

Study area

My study area was the Central Plains Experimental Range, located approximately 60 km northeast of Fort Collins, Colorado. The climate is semi-arid, with mean monthly temperatures ranging from -5°C in January to 22°C in July and 321 mm of annual precipitation (Milchunas and Lauenroth 1995). Vegetation is dominated by short, perennial grasses (*Bouteloua gracilis* and *Buchloe dactyloides*) interspersed with small shrubs and forbs (*Artemisia frigida, Eriogonum effusum, Sphaeralcea coccinea*), and prickly-pear cactus (*Opuntia polycantha*). At least three broad classes of vegetation and soil type can be recognized on the study area. Upland prairie is open grassland with small shrubs and cactus but no large woody shrubs. Soils are primarily fine sandy loams. Shrub grasslands occur alongside seasonal washes where soils are typically coarsely-textured (sandy loam or loamy sand). These areas support four-wing saltbush (*Atriplex canescens*), small shrubs (*A. frigida, E. effusum, Gutierrezia sarothrae, Ceratoides lanata, Chrysothamnus nauseosus*) and a variety of mid-grasses (*Pascopyron smithii, Stipa comata, Aristida longiseta, Sitanion hystrix*). A third vegetation type consists of a narrow (0.8-km wide) floodplain associated with two creeks. These areas have finely-textured loam soils with thick grass cover (*B. gracilis* and *P. smithii*) and large, dense saltbush. Upland sites are grazed by cattle in summer and fall, whereas saltbush sites are mostly grazed in winter and spring.

Most field work was conducted on two 2.72-ha trapping grids (12x12 stations with 15-m spacing) that were established in July 1992 in shrub-grassland and floodplain

vegetation. The shrub-grassland grid consisted of sparse saltbush (4% canopy cover) whereas saltbush was abundant (11% cover) on the floodplain grid. These sites were chosen for the present study because preliminary trapping revealed that grasshopper mice were relatively abundant on the shrub-grassland site but extremely rare on the floodplain grid (30 individuals vs. 3 individuals in >3000 trap-nights). In 1994, intensive studies of grasshopper mice were conducted on the shrub-grassland site, whereas the floodplain grid was used primarily for arthropod sampling.

Live-trapping, movements and habitat use

The trapping grid on the shrub-grassland site was expanded in January 1994 to 3.44 ha (18 rows by 10 columns). Because the primary objective of trapping in 1994 was to collect animals for tracking studies, I set only the three perimeter lines and six interior rows of traps, with a single large Sherman trap at each station (156 traps). Trapping was conducted for 3 consecutive nights during the dark phase of the lunar cycle in January, May, July, and October. Traps were baited in early evening with a mixture of peanut butter, oats, and bacon fat; raw cotton was provided to minimize trap mortality. I checked traps at dawn each morning and recorded sex, age and reproductive condition of each individual captured. Each mouse was marked with a uniquely-numbered aluminum ear tag (National Band and Tag Co., Lexington, Kentucky) and released at its capture location. Approximate age was estimated by mass and pelage characteristics (juveniles: uniform gray and <24 g; subadults: gray to gray brown, 24 - 26 g; adults: $\geq$ 26 g and/or with buffy brown wash) During January trapping, traps were wrapped with carpet and checked at ca. 2300 h and at dawn. Nighttime captures were transported to the field station until the dawn check to prevent hypothermia.

Individuals selected for tracking were removed from the trapping site and held at the field station in traps during the day. Mice were provided with extra bait and a slice of potato. Approximately 1-2 h before sunset, I dusted mice with fluorescent paint pigment (Radiant Color, Inc., Richmond, California) and released them at their capture locations (Lemen and Freeman 1985). Mice usually entered holes immediately, but because many switched

burrows before dark, I checked and marked the last daytime location of each mouse shortly after sunset to ensure that all movements recorded were nocturnal. I did not dust mice immediately following captures because preliminary studies indicated that grooming by mice often resulted in short, fragmented trails.

Beginning at ca. 2 h after dark, I followed powder trails from the final daytime location using a flashlight with an ultraviolet-light bulb (F6T5, General Electric Co., Cincinnati, Ohio). I marked trails with flagged nails at 1-m intervals for 100-m or until powder was no longer visible. I later surveyed trails with a theodolite and electronic distance meter (Pentax PTS-II05, Tokyo, Japan). Distances and turning angles from trails were used to calculate three movement indices: relative displacement, defined as the ratio of the straight-line distance of the trail to total trail length; mean vector length (Batschelet 1981); and fractal dimension (Mandelbrot 1983). Mean vector length ranges from 0 to 1.0 and described the tendency of mice consistently to move in a particular direction. Fractal dimension, calculated using the dividers method (Dicke and Burrough 1988), described the tortuosity of the trails and ranges from 1.0 for linear paths to 2.0 for convoluted trails that, if infinitely long, would fill a plane. Linear trails with little turning or reversals of direction therefore would tend to have low fractal dimension and high values for mean vector length and relative displacement.

Vegetation and substrate characteristics were measured at three scales along powder trails. At the finest scale, I recorded the cover type at each 1-m trail point, which likely reflected the ease of movement in different types of microhabitats. To describe microhabitat use along trails, I measured 13 vegetation and substrate characteristics at one random point from each 5-m segment of the trail. To describe habitat characteristics in the area surrounding the trail (intermediate scale), I recorded vegetation and substrate characteristics at a point located a random distance between 1 and 5 m to the left or right of the random trail points. Finally, to permit comparisons between habitats used by mice and random vegetation on the study areas (broad scale), I established transects of the same total length as trails at

random locations on the grid. Vegetation and substrate characteristics were recorded at both 1-m intervals (cover type) along the transect and at randomly-selected points from each 5-m segment.

I calculated the mean for each microhabitat variable for each trail, its adjacent points, and its associated random transect. To reduce the number of variables used in statistical tests, I performed principal components analysis (PRINCOMP procedure; SAS Institute 1989) on the mean values for microhabitat variables on trail and random transects. Because three variables measured on trails and transects were not recorded at adjacent points, I conducted a separate principal components analysis using only microhabitat variables from trails and adjacent points. Relative selection of microhabitats was determined by subtracting percent cover or principal component scores of random transects and adjacent points from those of the associated powder trails; I used paired t-tests to determine whether differences were significant. I also performed analysis of variance (GLM procedure) on difference values to examine seasonal trends in use of microhabitats. Microhabitat variables were transformed prior to statistical analyses (using natural logarithm, square-root, inverse, and arcsine-square-root transformations) to satisfy the assumptions of parametric tests; means and standard errors of non-transformed variables are presented throughout to facilitate comparisons.

Diet analysis

In 1994, I collected fecal pellets from traps of first-time captures of grasshopper mice on and near the shrub-grassland grid to describe seasonal variation in diet. Pellet samples were stored separately in 75% ethanol and refrigerated until laboratory analyses. Pellets from a sample were combined and a sub-sample of the homogenized pellets was mounted on a slide following the methods described in Hansen et al. (1974). Frequency of occurrence of plant and animal tissues was estimated in 20 random microscopic fields (Sparks and Malechek 1968) by the Composition Analysis Laboratory (Fort Collins, Colorado). To estimate taxonomic composition of arthropods in the diet, I counted the number of point intercepts of arthropod body parts in 20 random fields from each sample under low-power

(10-40 X) magnification. Recognizable structures (e.g., eyes, mandibles, antennae, limbs) were identified to ordinal or familial level using a reference collection. I multiplied the relative frequency of arthropod taxa times the proportion of animal matter to estimate percent composition by volume of these items in the diet.

Patterns of arthropod abundance

I conducted pitfall-trapping studies on the two trapping grids to estimate abundance and microhabitat distribution of terrestrial arthropods. Sixty-four pitfalls were placed in a systematic random design so that each one-sixteenth of the grid (0.81 ha) contained four traps, with one trap in each of four microhabitat types: shrub: beneath saltbush canopy; cactus: within a patch of prickly-pear cactus; grass: surrounded by grass; bare ground: in bare soil between vegetation. Pitfalls were plastic cups (90-cm diameter, 120-cm deep) buried flush with the ground surface. Opaque plastic funnels were suspended inside larger cups to shade traps and minimize escapes. I placed an additional 16 traps on mounds of northern pocket gophers (*Thomomys talpoides*) on the shrub-grassland site in 1994.

I checked traps over a period of 3 consecutive days on one occasion in spring (27 May - 10 June) and summer (28 July - 20 August) between July 1992 and May 1994. Trapping efforts were increased to approximately biweekly in July and August 1994. I summed the number of captures of arthropod taxa in the 16 traps in each microhabitat type over the 3-d period as an index of abundance in each microhabitat. Ants and other arthropods smaller than ca. 6 mm in length were not included in counts. I averaged the number of captures among the four microhabitats to estimate abundance on each study area. Paired t-tests were used to examine differences in arthropod abundance between sites, using the differences between captures in each microhabitat for a given sampling period. Seasonal variation in arthropod abundance was compared to air and soil temperatures recorded daily at a meteorological station approximately 5 km away. I also recorded the number of shrubs within a 2-m radius and the number of disturbances and burrows within 3 m of 50 random points on the trapping grids.

Because grasshoppers (Acrididae: Orthoptera) could escape from pitfall traps, I conducted flush counts on both study areas on seven occasions between June and August 1994, concurrent with pitfall trapping. I counted the number of grasshoppers flushed from 30-32 circular hoops (0.8-m^2 in area) placed at random on the grids. Counts were conducted during late-morning and early afternoon; sites were sampled within 1 h of each other on the same day.

Patterns of mouse abundance

I used a regression approach similar to that used by Morris (1987) to evaluate the roles of microhabitat versus macrohabitat variation on habitat selection. I live-trapped mice on 34 trapping areas during 1994 and 1995 to examine spatial variation in abundance in areas with different substrate and vegetation characteristics. These included nine 1.54-ha trapping webs (57 traps at 10-m intervals along 8 transects; Buckland et al. 1993), trapped for 4 consecutive nights in June 1994, and 25 0.32-ha rectangular plots (32 traps with 10 and 15-m spacing), trapped for 3 consecutive nights in June or July 1995. I estimated relative density by dividing the number of individuals captured by the effective trapping area to compare abundance among plots of different sizes. Trapping area was calculated by adding a 27-m strip to the area bounded by the traps. Strip width was one-half the average maximum distances between captures, estimated from other trapping studies (P. Stapp, unpublished data). Too few animals were captured to estimate density using population modeling procedures.

To describe microhabitats on trapping areas, I estimated the density of large shrubs ($\geq$ 0.30 m in height), small shrubs, burrows, and animal disturbances ($\geq$ 0.25 m^2 in area) within a 2-m radius of randomly-selected points on each site (28 random points for webs and 16 points for plots). I also recorded the area of the nearest disturbance and nearest large shrub as well as the percentage of bare ground within a 0.2-m^2 point frame. Principal components analysis was performed on natural log, square-root, or rank transformations of these variables. I also ranked each area by shrub abundance (1, 2, and 3 for upland prairie, shrub-grassland, and

floodplain, respectively) and increasing soil particle size (1 - 4 for loam, fine sandy loam, sandy loam, and loamy sand, respectively) to characterize macrohabitat on each site. Soil texture was not measured directly but was inferred from soil map units on Soil Conservation Survey maps (C. Yonker, Colorado State University, unpublished data). I included principal component scores for microhabitat variables and macrohabitat ranks in a stepwise multiple regression (REG procedure; SAS Institute, 1989) to determine which variables could best predict mouse abundance.

RESULTS

Live-trapping, movements and habitat use

Population density of mice on the shrub-grassland trapping grid was relatively low throughout 1994 and males and females were captured in approximately equal numbers (Table 3.1). Juvenile mice did not appear on the grid until mid-spring and most had apparently dispersed or died by autumn. The population appeared to turn over each year (Table 3.1); between 1992 and 1994, no mice captured in a given summer were recaptured the following summer. On my study area, most mice probably do not survive more than one winter, although one male first captured as an adult in December 1993 was recaptured consistently through August 1995, indicating a natural lifespan of at least 2 years.

I recorded 27 powder trails from 17 different individuals (10 males, 7 females) during the four tracking sessions in 1994. All but three of the mice (one in May, two in July) tracked were adults. Mice were tracked only once in a given session, but one female was tracked during all sessions, one male was tracked during three sessions, and five other mice were tracked during two sessions. However, because of the amount of time separating tracking periods, I considered trails to be independent for analyses.

Mice moved considerable distances before powder trails were no longer visible. Measurements of movements and habitat use were restricted to the first 100 m of trails but trails were often visible for longer distances, especially in spring and summer; two individuals were followed for more than 185 m. Trails were relatively linear and there were

no significant seasonal differences in movement indices (Table 3.1). Male mice tended to move more linearly (relative displacement: $\bar{x}$=0.63, SE=0.09) than females ($\bar{x}$=0.54, SE=0.04), but movement indices were not different between sexes (Wilcoxon test, P>0.137). However, net and total trail length were strongly correlated for males (Spearman r=0.87, P=0.0001) but not for females (r=0.31, P=0.331). Females therefore moved approximately the same net distance in all seasons, regardless of total trail length (Kruskal-Wallis test, P=0.533).

Principal components analysis produced four composite variables that described 74-83% of the variation in microhabitats along trails, adjacent points, and random transects. For the first three components, the magnitude and sign of the eigenvectors were similar between separate analyses for adjacent points and random transects (Table 3.2). The first component represented the amount and proximity of bare soil, animal disturbances, and burrows near the trail whereas trails with high scores for the second and third components were associated with large and small shrubs, respectively. Most animal disturbances (82%) were created by pocket gophers or other small mammals; the remainder were harvester-ant mounds. The fourth component represented the proximity and abundance of burrows but the signs of the eigenvectors were reversed for the two analyses (Table 3.2). Trails and adjacent points associated with burrows had high scores for the fourth component, whereas trails and transects with high burrow densities had low scores.

Comparisons between vegetation and substrate characteristics along trails and at random locations revealed preferences for disturbed soils and burrows at all spatial scales but little seasonal variation in habitat use (Tables 3.1, 3.3). Mice traveled on mounds more than expected based on the percent cover of mounds on the study area and from the area adjacent to trails. The selection of particular microhabitats was most apparent in winter and summer (Table 3.3). In both January and July, movements were associated with disturbances and away from shrubs, whereas mice remained relatively close to burrows in winter. Mice also entered burrows frequently during fall and winter (Table 3.1). On a broader scale, areas of

the grid used by mice had more disturbances and more burrows than random transects. Although mice showed no affinity for shrubs on a microhabitat scale, areas used by mice in July tended to have more saltbush than transects (Table 3.3). Conversely, in winter and spring, mice traveled in areas where large shrubs were relatively uncommon. Patterns of habitat use did not differ between sexes (Wilcoxon tests, $P>0.05$).

The movement characteristics of mice also reflected the use of microhabitats along trails. Mice that entered burrows more frequently and traveled more on mounds tended to have more convoluted trails (Spearman $|r|>0.41$, $P<0.030$). Densities of mounds and burrows were also generally lower on straight trails ($|r|>0.46$, $P<0.020$). The magnitude of the coefficient of variation in the distance from trails to shrubs, disturbances, and burrows reflected the tendency of mice to move toward or away from these objects. The coefficients of variation of the distances from trails to burrows and mounds were higher than that of both adjacent points and transects (Wilcoxon tests, $P=0.0001$), whereas the coefficient of variation for trail-to-shrub distances did not differ from that for adjacent points and transects ($P=0.655$). Furthermore, because trails were closer to mounds and burrows than random points and had higher densities of these features ($P<0.003$), mice appeared to orient towards mounds and burrows but not to large shrubs.

Diet analysis

I analyzed 53 fecal samples from 47 different individuals (24 males, 23 females) and each sample from a given season represented a different individual. Although four individuals contributed samples during more than one season, I considered samples from the same individual in different seasons to be independent because of the time elapsed between collection periods. Arthropods comprised 85.05% (SE=3.74) of the diet of grasshopper mice during the study period (Table 3.1). Neither the proportion of arthropods nor the proportion of seeds in the diet varied seasonally (Kruskal-Wallis test, $P>0.232$). The amount of plant tissue (stems, leaves, and flowers) in the diet differed among seasons, however, with the greatest proportion consumed in autumn (Table 3.1). Adult beetles (Coleoptera) constituted

38.61% (SE=7.32) of the diet and were the most common prey (>40% of the diet) in all seasons except winter ($\bar{x}$=17.67%, SE=3.17; P=0.002), when mice ate mostly crickets and grasshoppers (Fig. 3.1). Vertebrate remains (mammalian hair and bones) were found in only four of the 53 samples (7.55%; two winter, one spring, one summer) and comprised 7.35% (SE=3.20) of the diets of these mice.

Approximately 24% of the arthropod parts could not be placed into taxonomic groups, but 76% of the identifiable arthropods consisted of three families of adult beetles (Tenebrionidae, Scarabeidae, Carabidae), larval beetles and caterpillars (Lepidoptera), and orthopterans. There was no seasonal difference in the proportion of orthopterans or larvae consumed (P>0.05), although mice ate different types of larvae in different seasons (P=0.030). Beetle larvae were consumed primarily in winter ($\bar{x}$=2.95% of diet, SE=0.92), whereas mice ate caterpillars mostly in spring and summer ($\bar{x}$=2.58%, SE=0.56 and $\bar{x}$=3.42%, SE=1.43, respectively). The proportion of the three beetle families in the diet differed seasonally (P<0.030). The highest proportion of tenebrionids was consumed in autumn, the highest proportion of scarabs in spring, and there was no evidence of carabids in autumn or winter samples (Fig. 3.1). Diets of male and female mice generally did not differ (Wilcoxon tests, P>0.05), but females consumed more tenebrionids than did males during all seasons (analysis of variance, F=4.07, d.f.=7,45, P=0.002; season, sex effects, P<0.005; season*sex interaction, P=0.193).

Patterns of arthropod abundance

I restricted my analyses to the five insect groups (Tenebrionidae, Scarabeidae, Carabidae, Orthoptera, and larvae) that were the majority of the identifiable arthropods in grasshopper-mouse diets. Most captures of these taxa (82%) were tenebrionid beetles. The only orthopterans captured in pitfalls were sand and camel crickets (Gryllacrididae) and nearly all of the larvae captured were caterpillars.

Captures of insect prey in pitfalls differed between spring and summer and between the floodplain and shrub-grassland trapping areas. More insects were captured on the shrub-

grassland grid in spring and early-summer than on the floodplain grid, but captures became more similar on the grids as the summer progressed (Fig. 3.2a). The difference between floodplain and shrub-grassland areas in spring and early-summer resulted primarily from the higher numbers of tenebrionid and scarab beetles, crickets, and lepidopteran larvae. For instance, 87% (20/23) of scarabs were captured on the shrub-grassland grid; 15 of these captures occurred in May. Grasshoppers also were much more abundant on the shrub-grassland grid (2.59±0.49 grasshoppers /m^2) than on the floodplain site (0.70+0.13; paired t-test, n=7 counts, P=0.006).

For all but one trapping period, more insects were captured on gopher mounds than in any other microhabitat (Fig. 3.2b). Tenebrionid and scarab beetles and crickets, common prey of grasshopper mice, were frequently captured in traps on mounds. Traps under saltbush also usually had more captures than other microhabitats, especially in summer (Fig. 3.2b). Note that captures on gopher mounds exceeded those on bare soil during all trapping periods, suggesting that insects were attracted to soil friability rather than soil temperature or the lack of vegetation (Fig. 3.2b). Arthropod activity in all microhabitats had decreased markedly by October, when minimum temperatures near the surface were near freezing (Fig. 3.3).

Differences in abundance and activity of arthropods may reflect the relative availability of refuges on floodplain and shrub-grassland grids. The floodplain grid had a higher density of large shrubs than the shrub-grassland site (0.74±0.05 vs. 0.12±0.02 shrubs/ m^2) but many fewer mounds (120.14±35.34 vs. 522.97±92.58 mounds/ ha) and visible burrows (98.94±42.76 vs. 501.77±80.21 burrows/ ha). The soil is frozen from approximately November to April and arthropods must remain at least 20-50 cm below ground to avoid sub-zero temperatures (Fig. 3.3). Animal disturbances and burrows therefore may provide overwintering arthropods with access to subterranean thermal refuges. These refuges also may be important during warmer periods of the year, but insects may use litter or vegetation on the surface to avoid cool nighttime temperatures.

Patterns of mouse abundance

Population density reflected variation in both microhabitat and macrohabitat characteristics on trapping areas. On a microhabitat scale, mouse abundance was positively correlated with the density of burrows, mounds, and small shrubs, and the area of the nearest disturbance (Pearson $|r|>0.36$, $P<0.036$); burrow and mound density were the variables most highly correlated with population size ($r>0.67$, $P=0.0001$). Two principal components explained 65% of the variation represented by the seven microhabitat variables (Table 3.4). Sites with high scores for the first component had high densities of burrows, disturbances and small shrubs and more bare soil, whereas sites with high scores for the second component were associated with high densities and cover of shrubs (Table 3.4). The first principal component was highly correlated with both soil and shrub macrohabitat types, whereas the second component was positively correlated to shrub macrohabitats and not related to mouse density or soil texture (Table 3.5). The first principal component (NPC1) was the only variable selected by multiple regression (Table 3.5). However, removing the effects of NPC1 by partial correlation strongly affected the relationship between density and soil type (partial $r=0.24$, $P=0.181$), and removing the effects of soil type influenced the relationship between NPC1 and density (partial $r=0.331$, $P=0.060$). The abundance of mounds and burrows was particularly important on less friable, sandy-loam soils (Fig. 3.4). Thus, even though microhabitat variation was the best predictor of mouse density, the strong dependence of NPC1 on soil particle size suggests that soil type may also be an important factor on a macrohabitat scale (Fig. 3.4).

DISCUSSION

My results suggest that the proximate cues used by individual grasshopper mice to select foraging habitats are similar to those that govern the local abundance of mice on shortgrass-prairie landscapes. On a behavioral scale, mice traveled more on gopher mounds and in burrows than expected based on the abundance of these microhabitats, both in the area immediately surrounding powder trails and on the trapping grid as a whole. Furthermore,

mice appeared to orient their movements toward mounds and burrows and to concentrate their activity in areas where these microhabitats were dense. At the population level, mice apparently selected habitats largely on the abundance and characteristics of mounds and burrows rather than on broad-scale macrohabitat features such as the presence of shrubs or soil type. The close relationship between mound and burrow density and soil texture, however, implies that it may difficult to separate the roles of microhabitat and macrohabitat for wide-ranging species such as grasshopper mice.

Several authors (Egoscue 1960, Kaufman and Fleharty 1974) have proposed that grasshopper mice use disturbed soils primarily for grooming, but seasonal patterns in food habits, combined with the spatial and temporal variation in insect abundance, suggest that, in my study, mice may also have selected microhabitats based on prey availability. Captures of insects commonly consumed by mice were consistently higher in traps on gopher mounds than in other microhabitats. The difference in captures among traps was most pronounced in late spring, when mice used mounds most often. Captures of arthropods in shrubs and mounds became more similar as summer progressed, and although mice did not prefer shrub microhabitats, locations used by mice in summer had more shrubs than expected based on the amount of shrub cover on the site. By autumn trapping, soil-surface temperatures were relatively cold and surface activity of arthropods had declined markedly. Patterns of soil temperature suggest that insects and soil-dwelling larvae would have to be >20 cm below the surface to avoid freezing temperatures. I did not sample arthropods in winter, but gopher and ground-squirrel (*Spermophilus tridecemlineatus*) burrows seem like probable overwintering locations because many of the burrows constructed by these species occur at or below these depths (Jones et al. 1983, Wade 1950). For example, I have frequently observed grasshopper nymphs and adult beetles on the surface during periods of warm weather in January and February (P. Stapp, pers. obs.), and it seems unlikely that these insects emerged from frozen soil. Given that mice continued to consume primarily insects throughout the year, prey availability may explain their increased use of burrows during autumn and winter.

Seasonal patterns of arthropod abundance between floodplain and shrub-grassland areas also suggest that mice responded primarily to microhabitat variation in the prey availability. Prey were more abundant on the shrub-grassland grid during late spring and early summer, but, except for grasshoppers, summer captures of insects in the four microhabitats were similar on the two grids. Because orthopterans were not particularly important in summer diets, differences in arthropod numbers probably were not sufficient to explain the differences in grasshopper mice between floodplain and shrub-grassland grids. Instead, microhabitat affinities of mice may have reflected improved access to and, possibly, higher concentrations of prey in mounds and burrows, which were four to five times more abundant on the shrub-grassland grid.

Although the relationships among habitat use, diet, and arthropod abundance provide compelling evidence for the importance of prey availability, there are alternative explanations for my results. For example, mice may be able to move more rapidly on bare ground than on vegetation, and gopher mounds presumably are excellent dust-bathing sites. Dust-bathing cannot explain the extensive use of burrows, but burrows may serve as refuges from severe weather or predators, particularly in the absence of significant vegetative cover. If predation risk were a significant determinant of habitat use by grasshopper mice, however, then one might expect grasshopper mice to use shrubs more frequently. For example, deer mice (*Peromyscus maniculatus*) are morphologically similar to grasshopper mice and, like many quadrupedal rodents (Kotler and Brown 1988), prefer the cover of saltbush and other large shrubs (Chapter 2). Nevertheless, deer mice are consumed regularly by great horned owls (*Bubo virginianus*), whereas grasshopper mice are uncommon in owl pellets on my study area (Zimmerman et al. in press) and in the diets of many predators (e.g., Bailey and Sperry 1929, Egoscue 1960, 1962). Given the relatively low densities at which grasshopper mice typically occur, and that these mice are often the only nocturnal rodents present in shrub-free areas of shortgrass prairie (Lindquist et al. 1995), risk of predation may be lower on open prairie because it may not be profitable for owls and other predators to forage in these areas.

My results have several implications for our understanding of the role of small animals in grassland ecosystems and for other studies of habitat selection of small mammals. First, although grasshopper mice apparently selected habitat based on the distribution of disturbances and burrows, the abundance of these microhabitats ultimately reflects the response of fossorial and semifossorial animals to variation in vegetation and soil characteristics at somewhat larger spatial scales (Vaughn 1967, Moulton et al. 1983). Grasshopper mice excavate their own burrows in sandy soils (Ruffer 1965) but may depend on burrow systems created by other mammals for access to subterranean resources in areas of compact soils or dense mats of vegetation (Bailey and Sperry 1929). Mounds and burrows may be important for other vertebrates and arthropods on shortgrass prairie as well (Vaughn 1961). The effects of gophers and other burrowing rodents on productivity, nutrient dynamics, and diversity of both plants and animals are well-documented for many grassland ecosystems (Huntly and Inouye 1988, Whicker and Detling 1988, Hawkins and Nicoletto 1992). Fewer studies have examined the impact of fossorial mammals on shortgrass prairie (e.g., Grant et al. 1980, Martinsen et al. 1990), but my results suggest that the activities of these species play a significant role in the ecology of other consumers. These species may be particularly critical on shortgrass prairie because of the lack of substantial vegetative cover, especially during periods of harsh weather conditions common in northern regions.

Finally, my findings that grasshopper mice responded primarily to microhabitat heterogeneity in resources are consistent with many other studies of habitat use of small mammals (e.g., see reviews by Kaufman and Kaufman 1989, Kotler and Brown 1988, Reichman and Price 1993). Conversely, Morris (1987) argued that the population dynamics of rodents inhabiting temperate-zone forests and grasslands may be best understood by measuring resource availability on a macrohabitat rather than microhabitat scale. He suggested that the abundance of resources such as grass, acorns, and vegetation architecture likely varies more among macrohabitats than within a given site. These resources may be concentrated in local patches, but patches may be ephemeral and not restricted to a particular

microhabitat type (Morris 1987). Herbivorous and omnivorous rodents thus may encounter patches in proportion to their abundance, which may result in a positive relationship between overall resource abundance and population size.

The differences between patterns of habitat selection described by Morris (1987) and those observed in the present study and in many studies of habitat selection of desert heteromyids (Reichman and Price 1993) suggest differences in the persistence and predictability of resources in arid and semi-arid regions compared to more productive, complex environments. Although unpredictable at a given time or location, arthropods and seeds may be more concentrated and more accessible in some microhabitats (e.g., mounds, burrows, and shrubs) than others. My data indicate that, depending on abiotic conditions, this may be the case for nocturnal distributions of insect prey, and that in structurally simple environments where refuges are limited, insects and rodents prefer similar microhabitats, albeit for different reasons. Furthermore, compared to food resources such as seeds, the quantity of insect prey at a given microsite may be renewed frequently because insects may switch locations over time. If rodents can successfully associate microhabitat cues with higher probability of locating and capturing prey efficiently, then foraging patterns will appear to be more coarsely grained and reflect the abundance and distribution of these microhabitats. The aggregated spatial distribution of these microhabitats at larger spatial scales (i.e., between macrohabitats, P. Stapp, unpubl. data) therefore may determine patterns of local abundance of grasshopper mice. These findings demonstrate that measurements of habitat use and resource distributions at a variety of spatial and temporal scales are needed to evaluate the scaling of habitat selection and to identify potential mechanisms responsible for these patterns.

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Table 3.1. Summary of demographic, movements, microhabitat-use, and diet-composition parameters of northern grasshopper mice during 1994 field studies. Percentage of burrows is the number of burrows entered as a percentage of the number of trail points. Values in parentheses are standard errors of means. Of movement and microhabitat-use parameters, only percentage of burrows differed among seasons (ANOVA, $P<0.001$). Of diet parameters, only percentage plant tissues differed among seasons (ANOVA, $P=0.003$). Entries sharing letters are not statistically different (Tukey's HSD tests, $P>0.05$).

Parameter	January (Winter)	May (Spring)	July (Summer)	October (Autumn)
Demography				
Density (individuals /ha)	1.62	1.37	1.88	1.03
Sex ratio (M:F)	7:5	5:3	6:5	3:3
Percentage juveniles	0	25.00	45.45	0
Percentage recaptures[1]	8.33	50.00	45.45	66.67
Movements				
Number tracked (M:F)	5:3	3:2	4:4	3:3
Total trail length (m)	70.32 (8.62)	97.88 (4.04)	101.63 (0.81)	70.87 (10.97)
Relative displacement	0.60 (0.06)	0.76 (0.09)	0.52 (0.06)	0.51 (0.13)
Mean vector length	0.81 (0.02)	0.86 (0.03)	0.77 (0.02)	0.80 (0.04)
Fractal dimension	1.16 (0.02)	1.10 (0.02)	1.17 (0.02)	1.22 (0.05)
Microhabitat use				
Percentage of burrows*	7.60 (1.39)ab	1.53 (0.69)c	4.00 (1.12)bc	11.49 (2.29)a
Percentage of points in:				
animal disturbances	13.81 (3.28)	14.35 (4.50)	12.25 (2.82)	13.55 (3.23)
bare soil	33.03 (2.78)	42.91 (4.64)	31.25 (2.20)	34.56 (3.49)
large shrubs	1.30 (0.50)	0.73 (0.73)	0.87 (0.29)	1.06 (0.53)
small shrubs	0.91 (0.45)	0.44 (0.27)	0.87 (0.48)	1.64 (0.92)
shortgrass	62.29 (5.34)	45.80 (4.35)	62.50 (2.46)	53.53 (5.93)
midgrass	0.90 (0.52)	2.89 (1.38)	0.50 (0.27)	2.81 (1.69)
litter/debris	3.40 (1.14)	3.29 (1.45)	2.50 (0.89)	4.01 (2.04)

Table 3.1. continued.

Diet composition				
Sample size (M:F)	5:6	11:10	8:7	3:3
Percentage arthropods	87.40 (2.77)	85.48 (4.22)	92.55 (1.81)	74.76 (8.30)
Percentage seeds	6.16 (2.79)	9.75 (3.97)	4.96 (1.51)	8.47 (3.70)
Percentage plant tissues*	6.44 (1.68)a	4.08 (0.58)ab	2.33 (0.76)ab	16.77 (7.78)ac

1 animals marked in a previous session; for January, the site was trapped in July 1993.

Table 3.2. Eigenvectors for variables describing vegetation and substrate in principal components analysis of powder trails of northern grasshopper mice and on random transects. Variables were measured at randomly-selected points within 5-m segments of trails and transects. Percent cover of shrubs, bare soil, and grass were measured within a 0.24-m^2 point frame at each point. Average inter-shrub distance was the average of the distance from the nearest shrub to its three nearest neighbors. Large shrubs were ≥ 0.3-m in height; disturbances were ≥ 0.25-m^2 in area. Four components had eigenvalues greater than 1.0 and were included in analyses.

	TRAIL vs. ADJACENT				TRAIL vs. TRANSECT			
Variable	APC1	APC2	APC3	APC4	TPC1	TPC2	TPC3	TPC4
Number of shrubs within 1-m	0.15	0.57	0.09	-0.37	0.16	0.44	-0.01	0.25
Distance to nearest large shrub (m)	-0.24	-0.50	0.14	0.23	-0.20	-0.47	0.23	-0.09
Average inter-shrub distance	-	-	-	-	-0.25	-0.43	0.11	0.01
Area of nearest large shrub	-	-	-	-	0.15	-0.20	0.39	0.06
Number of small shrubs within 1-m	0.09	-0.10	0.60	0.38	0.16	-0.14	0.58	0.16
Percentage shrub cover	0.20	0.29	0.55	0.10	0.27	0.21	0.36	0.41
Number of disturbances within 1-m	0.40	-0.13	-0.14	0.02	0.33	-0.11	-0.28	-0.05
Distance to nearest disturbance (m)	-0.43	0.20	0.03	0.35	-0.38	0.22	0.19	-0.02
Area of nearest disturbance	-	-	-	-	0.08	-0.34	-0.37	0.38
Percentage bare soil	0.34	-0.44	-0.07	-0.25	0.35	-0.28	-0.20	-0.01
Number of burrows within 1-m	0.29	0.11	-0.37	0.55	0.30	-0.01	0.15	-0.54
Distance to nearest burrow (m)	-0.37	-0.20	0.21	-0.41	-0.35	-0.09	-0.09	0.47
Percentage grass cover	-0.43	0.17	-0.31	0.06	-0.40	0.14	-0.06	-0.25
Percentage variance explained	34.62	19.66	18.15	10.57	31.93	19.76	13.39	9.21

Table 3.3. Relative use of microhabitats by grasshopper mice. Entries are the difference between microhabitat variables on trails and those recorded at random points adjacent to trails or random transects. PC1-4 correspond to composite variables in Table 2. Asterisks and crosses associated with numerals indicate differences significantly different from zero (paired t-tests). Symbols alongside variables denote significant seasonal variation in the difference between trails and random points (analysis of variance). Entries with same letters are not significantly different (Tukey's HSD; P>0.05).

Comparison	January (Winter)	May (Spring)	July (Summer)	October (Autumn)
TRAIL - TRANSECT				
a) Fine scale (percent cover)				
Disturbances	12.44 (3.49)†	14.15 (4.34)***	10.37 (2.82)***	12.03 (3.34)**
Bare soil	19.48 (3.65)†	28.18 (6.11)***	19.12 (2.19)†	21.50 (4.51)***
Large shrubs	0.19 (0.67)	0.09 (0.63)	-0.25 (0.49)	-1.52 (0.99)
Small shrubs	-0.23 (0.44)	-0.56 (0.63)	-2.37 (1.53)	0.34 (1.22)
Shortgrass*	-10.62 (7.00)	-31.52 (5.70)†	0.37 (5.58)	-15.44 (10.81)
Midgrass*	-3.24 (1.57)	2.24 (1.59)	-12.62 (5.00)**	-5.03 (5.55)
Litter/debris	1.32 (1.03)	3.29 (1.45)**	0.50 (0.84)	1.95 (2.58)
TRAIL - ADJACENT				
b) Intermediate scale (5-m points)				
APC1	1.73 (0.59)**	1.62 (0.49)**	1.93 (0.51)***	2.73 (0.50)†
APC2	-1.02 (0.45)*	-0.55 (0.21)*	-0.73 (0.31)**	-0.35 (0.45)
APC3	-1.01 (0.45)*	-0.28 (0.37)	-0.38 (0.14)**	-0.49 (0.59)
APC4 **	1.35 (0.28)†ab	0.08 (0.41)ac	0.30 (0.18)a	0.79 (0.36)*a
TRAIL - TRANSECT				
c) Broad scale (5-m points)				
TPC1	1.90 (0.78)**	3.27 (0.40)†	2.43 (0.88)**	1.26 (1.10)
TPC2 †	-2.48 (0.52)†ab	-1.52 (0.65)*a	0.86 (0.41)*ac	-1.11 (0.96)a
TPC3	0.49 (0.39)	0.19 (0.27)	-0.42 (0.38)	0.37 (0.71)
TPC4	-1.29 (0.67)*	0.91 (0.50)	-0.73 (0.41)	-1.02 (0.46)*

* $P \leq 0.10$; ** $P \leq 0.05$; *** $P \leq 0.01$; † $P \leq 0.005$.

Table 3.4. Eigenvectors from principal components analysis on microhabitat variables measured on trapping areas. Variables were transformed prior to analyses. Two components had eigenvalues greater than 1.0.

Microhabitat variable	NPC1	NPC2
Density of large shrubs	-0.26	0.55
Density of small shrubs	0.46	-0.19
Density of burrows	0.44	0.32
Density of animal disturbances	0.44	0.43
Area of disturbance	0.41	-0.11
Area of large shrubs	-0.06	0.60
Percentage bare soil	0.40	-0.04
Percent variance explained	43.35	21.84

Table 3.5. Results from Pearson correlation analysis and stepwise regression describing relationships between grasshopper-mouse densities and microhabitat and macrohabitat variables on 34 trapping areas. Significance values associated with correlation coefficients are given in parentheses. NPC1 and NPC2 are the first two principal components resulting from analysis of microhabitat variables shown in Table 4. SHRUB and SOIL are the macrohabitat variables describing shrub abundance and soil texture. NPC1 was the only variable meeting the criteria for entry into the stepwise regression (alpha level to enter and remain=0.10).

a) Pearson correlation

	SHRUB	SOIL	NPC1	NPC2
Mouse density	-0.35 (0.044)	0.62 (0.0001)	0.64 (0.0001)	0.16 (0.363)
SHRUB		-0.52 (0.001)	-0.56 (0.0005)	0.61 (0.0001)
SOIL			0.78 (0.0001)	0.20 (0.261)

b) Stepwise regression - NPC1

	df	Mean square	F	P	R^2
Regression	1	0.271	22.79	0.0001	0.416
Residual	32	0.380			

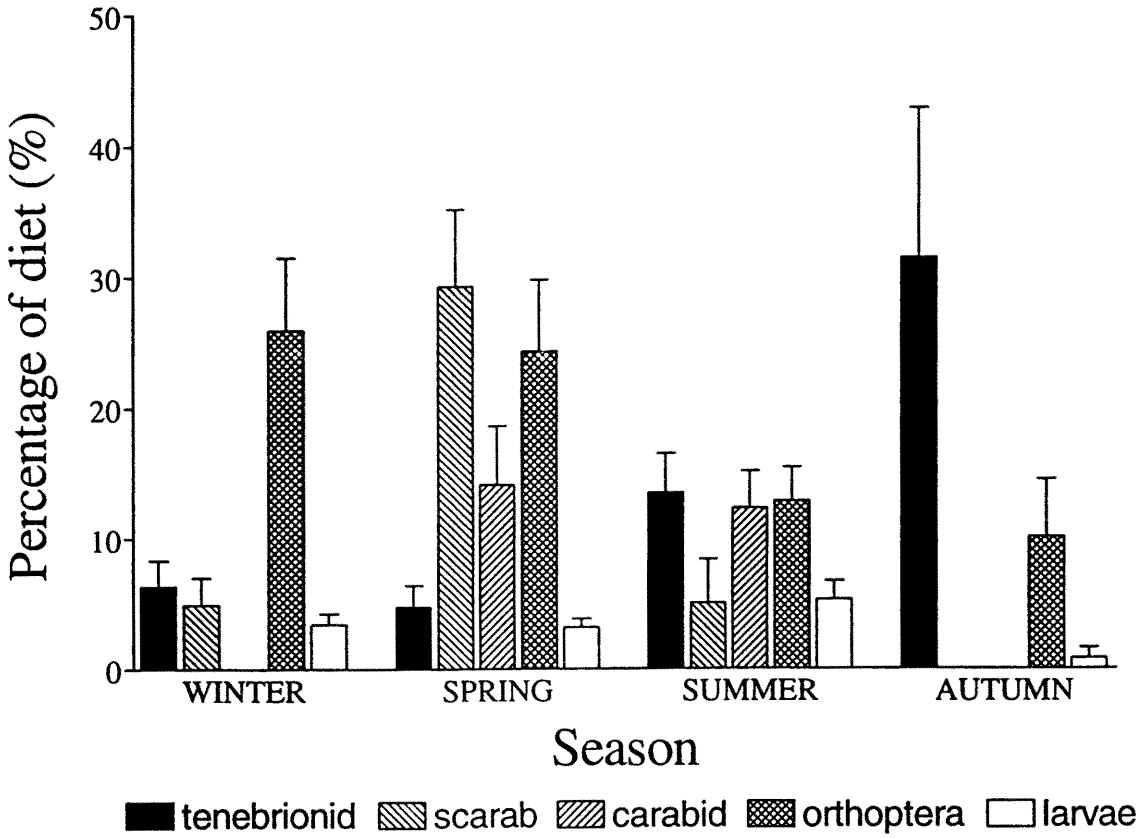

Fig. 3.1. Percentage by volume of arthropod taxa in diets of northern grasshopper mice on shortgrass prairie. Fecal pellets were collected in winter (January), spring (May), summer (July) and autumn (October) 1994. Values are means plus one standard error. Larvae category includes both coleopteran and lepidopteran larvae. See Table 1 for sample sizes.

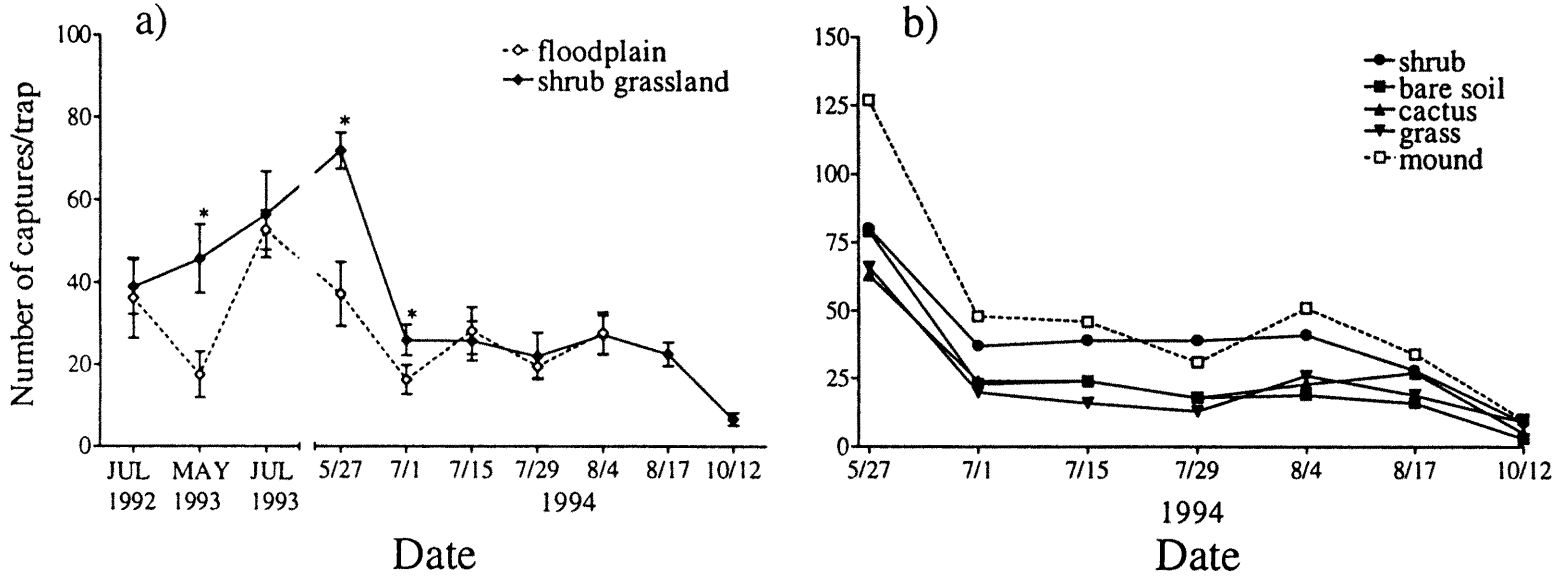

Fig. 3.2. Relative abundance of major arthropod prey captured in pitfall traps on the Central Plains Experimental Range. Insects represented are three beetle families (Tenebrionidae, Scarabeidae, Carabidae), lepidopteran and coleopteran larvae, and crickets (Gryllacrididae: Orthoptera). a) mean (± SE) number of captures in four microhabitat types (n=16 traps per microhabitat) on floodplain and shrub-grassland trapping areas between 1992 and 1994. Asterisks indicate significant differences between sites (paired t-tests, $P<0.05$). b) number of captures in five microhabitat types on the shrub-grassland trapping grid in 1994. Values are total number of insects captured over a 3-d period in each microhabitat.

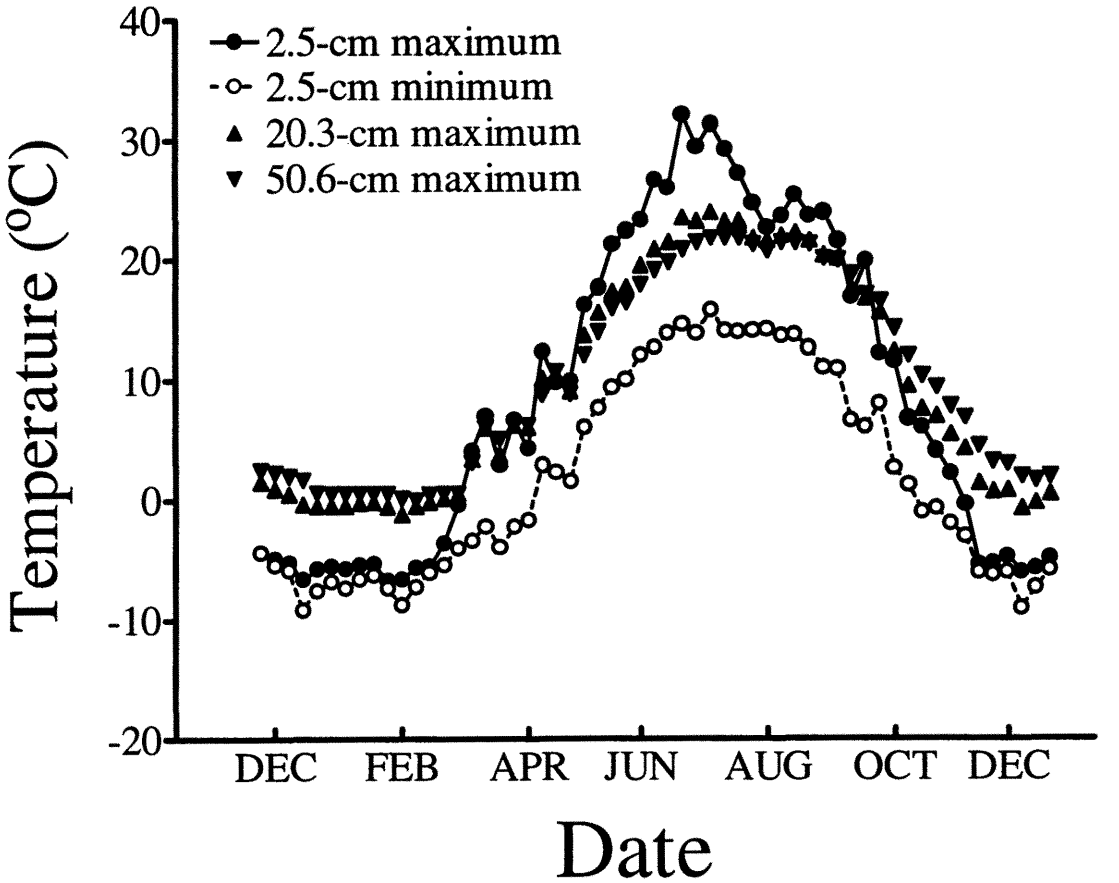

Fig. 3.3. Air and soil temperatures at the Central Plains Experimental Range between December 1993 and December 1994. Values are weekly means of measurements taken daily at a meteorological station of the Shortgrass Steppe Long-Term Ecological Research project. Solid and dotted lines represent maximum and minimum air temperatures, measured ca. 1.5 m above the ground. Maximum soil temperature was measured at 2.5 cm (near surface), 20.3 cm (approximate depth of pocket-gopher burrow) and 50.6 cm (ground-squirrel burrow) below ground. Minimum soil temperature was measured at 2.5 cm below ground.

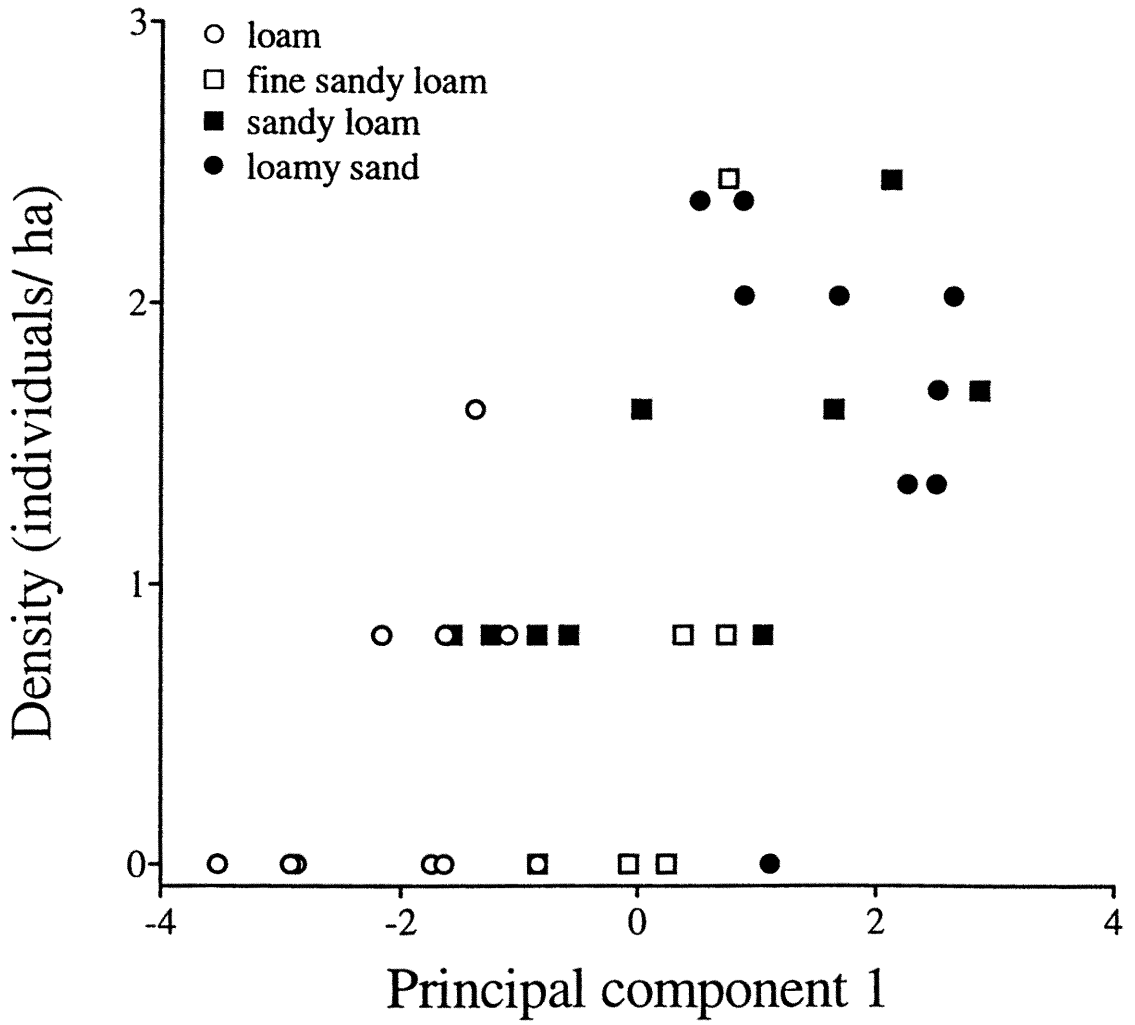

Fig. 3.4. Population density of northern grasshopper mice on sites with differing microhabitats. Values for principal component 1 derived from analysis of microhabitat variables on 34 trapping areas (Table 3.4). Sites are coded by soil type.

CHAPTER 4

COMMUNITY STRUCTURE OF SHORTGRASS-STEPPE RODENTS: THE ROLES OF INTRAGUILD PREDATION AND COMPETITION

ABSTRACT

Local assemblages of rodents on shortgrass steppe may reflect predatory or competitive effects of northern grasshopper mice (*Onychomys leucogaster*) on other species such as deer mice (*Peromyscus maniculatus*). I compared the abundance, microhabitat use, and diet of *P. maniculatus* on four areas of shrub-dominated prairie in north-central Colorado to that on four similar sites where I had removed *O. leucogaster*. The abundance of *P. maniculatus* decreased during the study on both control and removal sites, but the decline was greater on control sites, where numbers of *O. leucogaster* increased. Declines in the abundance of *P. maniculatus* on individual study plots were correlated with *O. leucogaster* abundance and recolonization. Only 6% of *P. maniculatus* present on controls during pre-removal trapping were captured 7 weeks later, compared to 32% of those initially present on removals. *P. maniculatus* increased their use of shrubs on controls, but no shift in microhabitat use was detected on removals. The proportion of arthropods in the diets of *P. maniculatus* and *O. leucogaster* was similar prior to removals, and although *P. maniculatus* consumed fewer arthropods after *O. leucogaster* were removed, diets did not differ between control and removal sites. In addition, Ord's kangaroo rats (*Dipodomys ordii*) increased slightly in number following removals and western harvest mice (*Reithrodontomys megalotis*) colonized two removal sites. These results suggest that intraguild predation or interference by *O. leucogaster*, rather than exploitative competition, influences the local abundance and

distribution of *P. maniculatus* and other small rodents on areas of shortgrass steppe where habitat characteristics permit coexistence. This study provides additional evidence for the role of predation risk as a determinant of rodent community structure.

INTRODUCTION

Studies of rodent communities have provided valuable insights into the importance of species interactions in shaping natural assemblages (Rosenzweig 1989). While early efforts focused largely on investigating the role of interspecific competition (Dueser et al. 1989), more recently researchers have emphasized that predators may also influence population and community dynamics, by selectively removing certain individuals or taxa and by modifying prey behavior (e.g., Longland and Jenkins 1987, Brown et al. 1988, Dickman et al. 1991, Dickman 1992, Kotler et al. 1994, Batzli and Lesieutre 1995). The notion that species differ in their responses to environmental heterogeneity and that this habitat partitioning permits coexistence is central to many studies of the effects of predation risk on community structure (Kotler and Brown 1988). Patterns of microhabitat use of similar syntopic species thus may reveal tradeoffs between their competitive abilities and vulnerability to predators. As a result of these tradeoffs, communities may reflect the effects of both predation and competition.

A traditional view of food-web dynamics is that competition operates within a trophic level, whereas predation operates between levels. As a consequence, predation and competition usually have been studied separately. In many ecological systems, however, one or more species may act as both a predator and competitor with other species at the same or similar trophic levels. This phenomenon, termed intraguild predation (Polis and McCormick 1986), has been studied most often in invertebrate communities (e.g., Polis et al. 1989, Spence and Cárcamo 1991, Johansson 1993, Rosenheim et al. 1993, Wissinger and McGrady 1993, Fincke 1994), but it may be widespread in communities of carnivorous and omnivorous vertebrates as well (e.g., Cortwright 1988, Polis et al. 1989, Szeinfeld 1991, Doncaster 1992, Gustafson 1993, Lindström et al. 1995, Olson et al. 1995). Here, I present evidence that predatory or agonistic activities of a carnivorous rodent affect the abundance and surface

activity of other small mammals, and I suggest that these interactions influence the structure of local rodent assemblages in North American grasslands.

Grasshopper mice (genus *Onychomys*) are unique among North American rodents in having a diet of primarily animal matter (McCarty 1978). Insects are their predominant prey but *Onychomys* also consumes small vertebrates, including other rodents (Bailey and Sperry 1929, Flake 1973). The largest (30 g) species, the northern grasshopper mouse (*Onychomys leucogaster*), inhabits desert and semiarid regions from central Canada to Mexico and is sympatric throughout its range with the deer mouse (*Peromyscus maniculatus*; Hall 1981). *P. maniculatus* is more omnivorous than *O. leucogaster* but its diet may contain >60% arthropods during spring and early summer when these prey are abundant (Flake 1973). Adults are one-third smaller than *O. leucogaster* (Armstrong 1972) and are known prey (Bailey and Sperry 1929, Flake 1973). Hence, interactions between these species may be both predatory and competitive in nature.

If *O. leucogaster* represents a threat to *P. maniculatus* and other rodents, then we might expect patterns of abundance and habitat use to reflect the abundance of *O. leucogaster*. For example, Rebar and Conley (1983) cited evidence of predation by *O. leucogaster* on Ord's kangaroo rats (*Dipodomys ordii*) and reported that *D. ordii* shifted microhabitat use in the presence of *O. leucogaster*. *D. ordii* are granivorous and approximately twice the size of *O. leucogaster* (Garrison and Best 1990). Given the small size and omnivorous habits of *P. maniculatus*, it seems likely that *O. leucogaster* exerts a similar or more significant impact on *P. maniculatus* in areas where they co-occur.

O. leucogaster and *P. maniculatus* are the most common nocturnal rodents on shortgrass steppe of the Central Plains (Abramsky et al., 1979; Grant et al., 1977). Preliminary studies conducted in north-central Colorado revealed that movements of *P. maniculatus* are closely associated with shrubs, whereas *O. leucogaster* travel on bare, disturbed soils and show no affinity for shrub microhabitats (P. Stapp, unpublished manuscripts). Shortgrass-steppe vegetation is dominated by short, perennial grasses, but

large shrubs are present in areas with coarsely-textured soils. Shrubs function as refuges from predators for quadrupedal rodents such as *P. maniculatus* (Kotler and Brown 1988) and may provide refuge from *O. leucogaster* as well.

I removed *O. leucogaster* from shrub-dominated areas of shortgrass steppe to examine the effects of this species on *P. maniculatus* and other resident small mammals. I predicted that if exploitative competition for food was important, then *P. maniculatus* would include more arthropods in their diet on removal sites and compared to untreated sites (controls). If *O. leucogaster* exclude *P. maniculatus* from particular habitats by interference, then removals should result in an increase in *P. maniculatus* and a shift into microhabitats previously used by *O. leucogaster*. Alternatively, the microhabitat affinities of *P. maniculatus* may reflect social interactions or the spatial distribution of resources and thus may be independent of the activities of *O. leucogaster*. In this case, the abundance and microhabitat use of *P. maniculatus* may not differ between removal and control sites. If predation by *O. leucogaster* affects *P. maniculatus*, however, then we might expect mice to select microhabitats where exposure to *O. leucogaster* is minimized, and should observe changes in *P. maniculatus* numbers that reflect the abundance of *O. leucogaster*. Furthermore, because other rodents also may be vulnerable to predation, removal of *O. leucogaster* may result in changes in their abundance as well.

STUDY AREA AND SPECIES

I conducted my experiments at the Central Plains Experimental Range in north-central Colorado, located approximately 60 km northeast of Fort Collins. Western portions of the Central Plains Experimental Range represented shortgrass prairie in the Grassland Biome of the US International Biological Program from 1968 to 1976 (Pawnee site), and the site currently serves as the primary location of the Shortgrass Steppe Long-Term Ecological Research project. The climate is semi-arid, with mean monthly temperatures ranging from -5 °C in January to 22 °C in July. The area receives an average of 321 mm of annual precipitation, most of which falls in brief spring and summer thunderstorms (Milchunas and

Lauenroth 1995). The topography consists of flat uplands separated by shallow swales and broad seasonal drainages. Upland vegetation is primarily *Bouteloua gracilis* and *Buchloe dactyloides* interspersed with *Opuntia polycantha* and numerous small shrubs (*Artemesia frigida, Eriogonum effusum, Guterrezia sarothrae, Ceratoides lanata*). Lowland areas typically have an abundance of large shrubs such as four-wing saltbush (*Atriplex canescens*) and intermediate-height grasses (*Pascopyron smithii, Stipa comata, Sitanion hystrix*). Most soils are sandy loam but loamy soils occur in seasonal drainages, where saltbush cover is greatest. Areas adjacent to these floodplains tend to have loamy-sand and sandy soils, less dense saltbush, and a mixture of grasses and small shrubs.

The density and diversity of shortgrass-steppe rodents are generally lower than in other North American grasslands (Grant and Birney 1979). Densities usually do not exceed 4 individuals/ ha, and both density and diversity are higher in shrub-dominated areas than on upland prairie (Lindquist et al. 1995). *P. maniculatus* and *O. leucogaster* comprise >70% of all nocturnal individuals captured; >90% of all captures are either these species or *Dipodomys ordii*. *O. leucogaster* inhabit both upland and lowlands, whereas *P. maniculatus* primarily occupy lowlands and are most abundant in saltbush areas. *D. ordii* are captured most often in mixed shrub-grassland areas, where soils are coarsely-textured and mid-grasses and small shrubs are common. Harvest mice (*Reithrodontomys megalotis*) tend to be restricted to areas with dense shrubs and grass and in weedy vegetation. Ground squirrels (*Spermophilus tridecemlineatus*) are present on all vegetation types, but are diurnal and were not usually captured during my studies.

METHODS

Population size and removal experiment

In June 1994, I established eight 1.54-ha trapping webs (Buckland et al. 1993) on lowland saltbush sites with Remmit loamy-sand soils. Webs were located < 100 m from floodplain areas with high shrub densities and, presumably high *P. maniculatus* densities, to permit immigration. Webs consisted of eight 70-m transects arranged as spokes from a

central point, with a Sherman live trap placed at each 10-m interval along transects (57 traps per web). I baited traps with peanut butter and oats and provided raw cotton for bedding. Traps were set at dusk and checked shortly after dawn. I recorded the sex, age, and reproductive status of each animal, gave each a uniquely-numbered ear tag, and released each at its capture location. I trapped each web for 4 consecutive nights in each session to estimate abundance and to capture *P. maniculatus* for tracking (see below). Four webs (two removals, two controls) were trapped concurrently.

Each web was trapped once in the pre-removal trapping session (7-15 June). I then randomly assigned four webs as removals and four as untreated controls. I removed *O. leucogaster* by trapping for 2-4 nights each week for the duration of the study. *O. leucogaster* were sacrificed by overdose of methoxyflurane (Metofane®, Pittman-Moore, Mundelein, Illinois). Sites were trapped again at 4 weeks (6-15 July) and 7 weeks (1-11 August) after the first removals. I used the minimum number of individuals alive (MNA; Krebs 1966) as an estimate of relative abundance because low numbers of captures precluded density estimation by distance sampling (Buckland et al. 1993). I estimated shrub density by recording the number of shrubs ($\geq$0.3-m in height) within a 2-m radius of 28 randomly-selected trap stations on each web.

All statistical procedures were performed in SAS (SAS Institute 1989). I used repeated measures analysis of variance (ANOVA) to examine changes in rodent abundances and included shrub density on webs as a covariate to account for differences in site vegetation. Linear contrasts were then performed to test the hypotheses that *P. maniculatus* and *D. ordii* were more abundant on removal sites than on controls following removal of *O. leucogaster*.

To estimate my ability to detect significant changes in *P. maniculatus* abundance during a given time period, I calculated the power of my experiment using the methods described by Dueser et al. (1989). I calculated the noncentrality parameter (δ) of the t-distribution as:

$$\delta = EMNA / \sigma\sqrt{(1/n_{control} + 1/n_{removal})},$$

where EMNA is the expected change in the MNA of *P. maniculatus*, σ is the standard deviation of the hypothesized effect and n is the number of replicates for each treatment (Dueser et al. 1989). Power values were obtained by comparing values for δ to those in Winer et al. (1991; Table D.13). I first calculated δ using pre-removal data, assuming complete and partial compensation for the number of O. *leucogaster* removed and assuming that all *O. leucogaster* would be removed. At the end of the experiment, I re-calculated power using post-removal values for *O. leucogaster* abundance, which reflected the effectiveness of my removals.

Microhabitat use

On the morning after the last night of trapping during a given session, I transported adult *P. maniculatus* from each web to the field headquarters, where they were held in traps and provided extra food and a slice of potato or apple. Individuals were selected to obtain approximately equal representation of sexes. Beginning 1-2 h before sunset, mice were dusted with fluorescent powder (Radiant Color, Richmond, California) and released at their location of capture. Dusted mice usually entered holes immediately, but because many switched burrows before dark, I checked and marked the last daytime location of each mouse shortly after sunset to ensure that all movements were nocturnal. Beginning at ca. 2 h after dark, I followed powder trails for 50 m using an ultraviolet lantern, starting at the last daytime burrow and marking the path at 1-m increments with flagged nails. A few mice that had not entered burrows by nightfall were located beneath shrubs; tracking of these mice began from the first burrow that they eventually entered. All tracking was performed during the dark phase of the lunar cycle.

To assess the response in microhabitat use of *P. maniculatus* to removal of *O. leucogaster*, I recorded 10 vegetation and substrate characteristics along powder trails (Table 4.1). Six of these variables measured the relative use of shrubs and four evaluated the use of soil disturbances [mounds of northern pocket gophers (*Thomomys talpoides*) and western

harvester ants (*Pogonomyrmex occidentalis*)] and burrows, microhabitats typically used by *O. leucogaster*. The percentage of bare soil and shrubs were recorded at each 1-m trail point. The remaining eight variables were measured at one random path point selected from each 5-m segment of the trail.

I performed a principal components analysis (PCA; PRINCOMP procedure) using the 10 microhabitat variables along each movement trail to reduce the number of variables necessary to describe microhabitat use. Data from both control and removal groups and the three sampling periods (pre-removal, post 4 weeks, post 7 weeks) were included in the PCA. I then conducted separate analyses on PCA scores to test treatment effects within each time period (nested ANOVA) and to examine shifts between pre-removal and post-removal sessions for a given treatment (repeated measures ANOVA). Microhabitat variables were transformed (square-root, arcsine square-root or logarithm) prior to analysis to achieve normality and homoscedasticity.

Diet overlap

During trapping sessions, I collected fecal pellets from traps of first-time captures of *P. maniculatus* and *O. leucogaster* to examine dietary overlap between these species and to document changes in *P. maniculatus* diet in response to removals. Diet was estimated from samples collected using eight *P. maniculatus* from removal sites and eight from controls in each trapping session. Whenever possible, samples from one male and one female from each web were analyzed; declines in abundance during the study led to unequal representation of webs, but every site was represented in all collections. I also analyzed samples from eight *O. leucogaster* collected from each treatment prior to removals, and from eight individuals from control webs during each of post-removal session.

Fecal samples were stored separately in 75% ethanol and refrigerated until laboratory analyses. Pellets from a sample were combined and a sub-sample of the homogenized pellets was mounted on a slide following the methods described in Hansen et al. (1974). Frequency of occurrence of plant and animal tissues was estimated in 20 random microscopic fields

(Sparks and Malechek 1968). Diet composition was quantified by the Composition Analysis Laboratory (Fort Collins, Colorado); laboratory personnel were not told which species provided samples. To estimate taxonomic composition of arthropods in the diet, I counted the number of point intercepts of arthropod parts in 20 random fields under low-power (10-40 X) magnification. Recognizable structures (e.g., eyes, mandibles, antennae, limbs) were identified to ordinal or familial level using a reference collection of common arthropods on the study area. I multiplied the relative frequency of arthropod taxa times the proportion of animal matter to estimate percent composition by volume of these items in the diet.

To investigate treatment-related differences in food habits, I compared the proportion of arthropods in *P. maniculatus* diets between control and removal sites for each time period separately using analysis of variance. I also used ANOVA to examine shifts in the percentage of arthropods in the diet after removals separately for each treatment group. Overlap between *P. maniculatus* and *O. leucogaster* was evaluated by comparing 95% confidence intervals around the mean for each treatment group during each time period. Values for percent composition were transformed by taking the arcsine square-root prior to analysis. Except where indicated, results presented are mean and one standard error (SE) of untransformed variables.

RESULTS

Population size and removal experiment

A priori power calculations indicated that the design of the experiment had high power. The average number of individuals alive (MNA) of *O. leucogaster* during pre-removal trapping on all eight webs combined was 5.37 individuals, and the average standard deviation of MNA of *P. maniculatus* was 1.25 individuals. Assuming complete compensation for the *O. leucogaster* individuals removed (EMNA=5.37, δ=6.07), power for a one-tailed test with α=0.05 and d.f.=6 was greater than 99%. Because rodent numbers were generally low, I also calculated power for replacement by one *P. maniculatus* for every two

O. leucogaster removed. Power (EMNA=2.68, δ=3.03) for the partial-compensation scenario was 84%.

Despite my frequent removals, MNA of *O. leucogaster* on removal webs at the end of the experiment was, on average, only 55% lower than during pre-removal trapping. I re-calculated power assuming a change in *P. maniculatus* equivalent to 45% of the *O. leucogaster* present prior to removals. Power for complete replacement (EMNA=2.42 individuals, δ=2.74, α=0.05, d.f.=6) declined to 78% and, for partial replacement (EMNA=1.41 individuals, δ=1.37), to 33%. Based on these results, I set α=0.10 to evaluate the significance of tests of changes in abundance.

P. maniculatus were more abundant on control sites than removals during pre-removal trapping (F=6.23, d.f.=1, P=0.047), but the number of *O. leucogaster* did not differ between treatments (F=0.32, d.f.=1, P=0.594; Fig. 4.1). My removals were effective at keeping *O. leucogaster* numbers lower, on average, on removal sites than on controls (one-tailed $P \leq 0.045$), although many new individuals immigrated to these sites (see below). Treatment effects did not differ between the two post-removal periods (linear contrast F=2.22, d.f.=1, P=0.196) and *O. leucogaster* were less numerous on removal sites than on controls following the initiation of removals (contrast between pre-removal and mean of post-removals, F=4.13, d.f.=1, P=0.052).

P. maniculatus decreased in numbers throughout the study period (F=3.78, d.f.=2, P=0.06) but changes in abundance differed among sites. The decline in abundance from pre-removal levels to the final trapping period was more pronounced on control sites than on removals (F=6.37, d.f.=1, one-tailed P=0.025) and most of this change occurred relatively quickly. By 4 weeks after the first grasshopper mice were removed, the number of *P. maniculatus* captured on controls dropped markedly from pre-removal levels but remained relatively constant on removal sites (contrast F=3.69, d.f.=1, one-tailed P=0.055; Fig. 4.1). On average, control sites lost three individuals by 4 weeks after removals began (a decline of 38%, SE=26), whereas there was no significant change in number of individuals on controls

(a 13% increase, SE=29). The rapid decline in *P. maniculatus* on controls corresponded to an increase in *O. leucogaster* at the 4-week trapping period (Fig. 4.1). By the end of the experiment, abundance of *P. maniculatus* was 64% (SE=10) lower on controls than during pre-removal sampling, compared to 35% (SE=21) lower on removals. Only 6% of the individuals present on controls during pre-removal trapping were captured 7 weeks later, compared to 32% of those initially present on removals.

Although there was no significant difference in shrub density between treatments (control $\bar{x}$=0.19 shrubs/m^2, SE=0.02; removal $\bar{x}$=0.18 shrubs/m^2, SE=0.02; t=0.274, d.f.=6, P=0.793), changes in *P. maniculatus* abundance was affected by the amount of shrub cover on trapping sites. Overall, the decline on controls was greatest on sites with the least shrub cover (Spearman r=0.95, P=0.051), whereas there was no significant relationship between shrub density and changes in population size on removals (r=0.40, P=0.600). The relative change in *P. maniculatus* numbers was negatively correlated with the number of *O. leucogaster* present prior to removals (r=-0.69, P=0.060); this relationship was most pronounced at 4 weeks after the first removals, the period of greatest change in *P. maniculatus* abundance (Fig. 4.2; r=-0.88, P=0.004). The relationship between changes in *P. maniculatus* abundance and initial numbers of *O. leucogaster* differed between treatments and with differences in shrub density, particularly on control sites (r=-0.95, P=0.051). In fact, the only control site where numbers rose rather than declined during the post-4-week sampling period was the site with the highest shrub density, and the only removal web to experience a decrease in abundance had the lowest shrub density of all the sites (Fig. 4.2).

I removed 73 *O. leucogaster* during the course of my experiment, including 45 adults [sex ratio (M:F)=31:14] and 28 juveniles (11:17). On average, 18 mice were removed from each trapping web (range 11 - 28), but because of the frequency of trapping, none presumably was present longer than 3-5 days. Most of the mice that immigrated to the sites were adult males (sex ratio=24:10) and juvenile females (9:15). Approximately 57% (39/69) of those removed had prominent rust-colored stains on their throats and chests that appeared to be

dried blood, suggesting that these mice consumed other vertebrates. Nearly 80% (31/39) of these were adults. Therefore, 71% of adults removed (31/44) had stained throats, compared to 32% (8/25) of juveniles. Furthermore, the decrease in number of *P. maniculatus* was most pronounced on removal sites where the most *O. leucogaster* were removed (Fig. 4.3) and this decline was greatest where re-colonization by adults was greatest (Spearman r=-0.95, P=0.051). I attempted to determine whether stains on the throats of *O. leucogaster* were mammal blood or from some other vertebrate, but too little residue remained for lab analyses.

Removal of *O. leucogaster* also affected abundance of other rodent species. *Dipodomys ordii* tended to increase in number throughout the study period and the removal of *O. leucogaster* resulted in a small but significant increase in the number of *D. ordii* captured (Fig. 4.1). Unlike *P. maniculatus*, there was no detectable change in *D. ordii* numbers on either treatment at the post-4-week trapping period (contrast, F=1.03, d.f.=1, P=0.40), but by the end of the experiment, *D. ordii* had increased slightly more in abundance on removal sites than on controls (contrast, F=1.69, d.f.=1, P=0.095; Fig. 4.1). *Reithrodontomys megalotis* was not captured during pre-removal censuses but was captured on two of the removal sites (one adult male at each site) during the final trapping period. No other nocturnal species were captured during the experiment.

Microhabitat use

I measured microhabitat use along 59 powder trails left by *P. maniculatus*. Individuals were tracked only once during a given sampling period, but five individuals (three from control webs, two from removals) were tracked in more than one time period. Because of the time elapsed between sampling periods, I considered trails to be independent.

Four principal components had eigenvalues greater than 1.0 and the first two axes explained 61% of the variation in microhabitat use. The first axis (PC1) explained more than three times the variance than any of the other three components and represented the use of shrub cover (Table 4.2). Mice with high negative scores for PC1 traveled near to shrubs and in areas with higher shrub densities. Positive scores for the second component (PC2) were

associated with trails close to soil disturbances (Table 4.2). PC3 was negatively associated with burrow density and positively associated with small shrubs, whereas PC4 depicted the relative use of bare soil.

Use of shrubs and soil disturbances was similar between control and removal sites prior to removals and at 7 weeks after removals (Fig. 4.4) and there were no differences between treatments for any PCA variables ($P>0.155$). Four weeks after removals, however, mice on controls traveled more closely to shrubs and in areas where shrubs were more dense than did mice on removals (Fig. 4.4a; $F=20.79$, d.f.=1, $P<0.0001$). Scores for other axes, including the use of soil disturbances, did not differ between treatments ($P>0.099$). Tests for shifts in microhabitat use between pre-removal and post-removal periods confirmed that mice on controls increased their use of shrubs at 4 weeks after removals ($F=5.53$, d.f.=1, $P=0.033$; Fig. 4.4a). On removal sites, the use of shrubs and disturbances did not change over time ($P>0.398$), but mice used areas with higher burrow densities and fewer small shrubs at 4 weeks post-removal than prior to removals (PC3: pre-removal $\bar{x}=0.69$, SE=0.51, post-4-weeks $\bar{x}= -0.76$, SE=0.37; $F=12.17$, d.f.=1, $P=0.003$). By 7 weeks after the first removals, microhabitat use was again similar to that measured during pre-removal tracking on both treatments ($P>0.128$).

Diet overlap

With the exception of five individuals that contributed fecal samples in more than one trapping session (two from control webs, three from removals), each sample represented a different individual. On average, arthropods comprised 85-97% of the diet of *O. leucogaster* (Fig. 4.5). Coleoptera and Orthoptera were the most common taxa consumed throughout the study (43-55% and 10-33%, respectively). Of the beetles taken, *O. leucogaster* ate Scarabeidae most often during the pre-removal period (16-33% of the diet), Carabidae throughout the study period (6-23%), and Tenebrionidae most during post-removal periods (12-16%). Overlap in the 95% confidence intervals between and among sampling periods

and treatments indicated that the proportion of arthropods in *O. leucogaster* diets did not differ during the experiment ($P>0.05$).

In the late spring prior to removals, *P. maniculatus* and *O. leucogaster* diets contained similar proportions of arthropods (Fig. 4.5). As with *O. leucogaster*, Coleoptera (primarily Scarabeidae) and Orthoptera were common prey of *P. maniculatus* at this time (Table 4.3), but they ate more larvae than did *O. leucogaster* (2-4%). The proportion of arthropods consumed by *P. maniculatus* did not differ between treatments during any period of the experiment ($P>0.353$; Fig. 4.5). Between pre- and post-removal trapping periods, however, *P. maniculatus* markedly increased their consumption of seeds and reduced their use of arthropods (Fig. 4.5; Table 4.3). Because of the high variability among individuals on a given site, however, pairwise comparisons between pre-removal and post-removal diets on a given treatment were not statistically significant ($P\geq0.089$). On average, the decline in the proportion of arthropods eaten occurred on removals as well as controls, so that by the post 4 week sampling period, *P. maniculatus* on control sites consumed fewer arthropods than did *O. leucogaster* (Fig. 4.5). *P. maniculatus* generally ate fewer arthropods than *O. leucogaster* on control sites throughout the study period (Fig. 4.5, $P<0.05$).

DISCUSSION

The results of my removal experiment suggest that predation or interference by *Onychomys leucogaster* contributed to a decline of *Peromyscus maniculatus* abundance, particularly on control sites. Even though trapping sites were located near floodplain areas where densities of *P. maniculatus* were presumably high, mice did not colonize removal sites but instead declined markedly on controls in association with an increase in *O. leucogaster*. *P. maniculatus* decreased in abundance throughout the study, but the decline was greatest on the control sites with the most *O. leucogaster* prior to removals and on removal sites where re-colonization by *O. leucogaster* was most pronounced. The diets of *P. maniculatus* and *O. leucogaster* were similar before removals, but the decrease in the proportion of insects

consumed by *P. maniculatus* was similar on control and removal sites. It is therefore unlikely that exploitative competition was responsible for the observed changes in abundance.

The positive response of two granivorous species (*R. megalotis*, *D. ordii*) to removal of *O. leucogaster* provides additional evidence for the importance of predation or interference rather than exploitative competition. Dietary overlap between these species and *O. leucogaster* is relatively small (Flake 1973), which implies that they occupy different foraging guilds than do *O. leucogaster* and *P. maniculatus,* and hence probably do not compete with these species for food. Furthermore, I have no evidence that the supply of arthropod prey was limited or depleted, especially since *O. leucogaster* is capable of eating insects that are otherwise defended against vertebrate predators (e.g., tenebrionid beetles, Tschinkel 1975). It therefore seems unlikely that *O. leucogaster* consume *P. maniculatus* or other rodents to reduce interspecific competition, as has been suggested in other comparisons of intraguild predation and competition (e.g., Wissinger and McGrady 1993, Fincke 1994). Rather, consumption by *O. leucogaster* of other rodents may simply be opportunistic predation directed at a profitable prey item that, in some instances, happens to use a similar resource (Polis et al. 1989).

Many species modify their behavior and habitat use in the presence of predators (Lima and Dill 1990) and the results from my tracking studies suggest that the presence of large numbers of *O. leucogaster* affected the surface activity of *P. maniculatus*. *P. maniculatus* did not shift microhabitat use on removal sites, but instead traveled more closely to shrubs and in areas of higher shrub densities when *O. leucogaster* were abundant. Because *O. leucogaster* show no affinity for shrub microhabitats, *P. maniculatus* may have moved farther into shrubs to avoid contact with the larger, carnivorous mice. The use of shrubs as refuges was consistent with changes in abundance; for a given treatment, the decrease in *P. maniculatus* abundance tended to be inversely related to shrub density (Fig. 4.3). The absence of a shift away from the use of shrubs on removal sites suggests that, on shortgrass steppe, *P. maniculatus* may have an innate affinity for shrubs that may be independent of the

activity of other rodent species. While my results cannot address the mechanism underlying this species' apparent preference for shrub cover, the use of shrubs by *P. maniculatus* in this and other studies of predation risk (e.g., Thompson 1982, Clarke 1983, Kotler 1984, Travers et al. 1988, Longland and Price 1991) underscores the potential utility of shrubs for avoiding predators. Shrubs may also provide refuge for *Reithrodontomys megalotis*, which are approximately one-third the size of *O. leucogaster* (Armstrong 1972) and avoid odors associated with *O. leucogaster* (Stapp and Van Horne 1996).

Although many mice had what appeared to be blood-stained throats, I have no direct evidence that *O. leucogaster* prey on *P. maniculatus* or other rodents. Of the 32 fecal samples from *O. leucogaster* that I examined, only two (6%) contained vertebrate remains. Both laboratory (Egoscue 1960, Ruffer 1968, Cole and Wolfe 1970) and field studies, however, have reported that *Onychomys* eat small mammals. Bailey and Sperry (1929), for example, found remains of *P. maniculatus*, *Dipodomys* sp., *Reithrodontomys* sp., and other rodents in stomachs of *O. leucogaster* and suggested that small mammals constitute 2-6% of the foods eaten. Mammalian tissues, including remains of *P. maniculatus* and *D. ordii*, comprised 9-10% of the animal remains in the diet of *O. leucogaster* during earlier work on my study area (Flake 1971).

Despite these results, fecal or stomach-content analyses may underestimate consumption of vertebrates because predation may be relatively infrequent and because *O. leucogaster* may selectively consume parts of their prey that are not readily preserved (Horner et al. 1965). The scarcity of hair on nestlings, for example, may make it difficult to quantify predation on litters or juveniles in burrows. Predation on whole litters may affect recruitment and hence population dynamics. Getz et al. (1992) reported that *Blarina brevicauda* prey upon nestling voles (*Microtus* spp.) in undefended nests, and Lomolino (1984) attributed a decline in insular populations of *M. pennsylvanicus* to predation by *B. brevicauda* on young animals. Additional studies are needed to determine the frequency and demographic consequences of this type of predation.

Although my results implicate *O. leucogaster* as a major factor in the decline in *P. maniculatus* numbers in 1994, the decrease in *P. maniculatus* on sites with and without *O. leucogaster* cannot be easily explained. In June, temperatures reached record-high levels and there was little precipitation; these factors may have reduced seed and arthropod production (P. Stapp, submitted manuscript), and as a consequence, *P. maniculatus* numbers. The abundance of granivorous *D. ordii* and insectivorous *O. leucogaster*, however, implies that resources may still have been plentiful. Weasels (*Mustela frenata*) were sighted more frequently in summer 1993 and spring 1994 than in previous and subsequent periods (P. Stapp, pers. obs.). Estimates of predator abundance were not available, but populations may have been elevated in response to high rodent densities in 1992 (P. Stapp, unpublished data). It is therefore possible that predators such as *M. frenata* (or *O. leucogaster*) could have been attracted to the abundance of *P. maniculatus* on controls (Fig. 4.1) and could have caused the rapid decline on these areas compared to removals. However, unless *P. maniculatus* are more vulnerable to predators than are other rodents, this hypothesis cannot explain the increase in *O. leucogaster* on controls or the relationship between declines in *P. maniculatus* numbers and *O. leucogaster* abundance.

This area-wide crash could have affected the outcome of my experiment if the persistence of local populations is dependent on dispersal from surrounding areas. For example, lower survival and reproductive success of *P. maniculatus* in years like 1994 may result in less recruitment from high-density areas. Individuals excluded by competitors or lost to predators therefore may not be replaced by immigration. Conversely, during years of normal or high survival and reproduction, predation by *O. leucogaster* may reduce local densities but sites may be quickly re-colonized by dispersers from adjacent areas. During periods and in areas where insect prey are plentiful, predation by *O. leucogaster* on other rodents may be mostly opportunistic. If so, then the relative impact of *O. leucogaster* predation on *P. maniculatus* may reflect spatial and temporal variation in the availability of arthropod prey and the juxtaposition and relative quality of *P. maniculatus* habitats.

In earlier research on my study area, Abramsky et al. (1979) suggested that interspecific competition among rodents affected community structure on experimentally-manipulated prairie. My experiment similarly underscores the importance of species interactions, but demonstrates that predation risk may also play a role in structuring the patterns of local abundance and distribution of resident small mammals. As in Abramsky et al. (1979), interactions between *O. leucogaster* and other rodents are mediated by heterogeneity in vegetation structure; shrubs may serve as refuges for *P. maniculatus* from *O. leucogaster* and, possibly, other predators. My results can not resolve whether *P. maniculatus*' affinity for shrubs is a consequence of perceived predation risk, but the activities of *O. leucogaster*, when abundant, seem to reinforce these tendencies. Additionally, the immigration of *R. megalotis* to removal sites suggests that this species' use of dense vegetation may in part reflect vulnerability to *O. leucogaster.*

At a somewhat larger scale, the patterns of distribution and abundance on shortgrass steppe reveal associations between rodent species and specific habitat features. As a consequence of these habitat affinities, the composition of a local assemblage ultimately reflects the ability of the habitat to satisfy the individual requirements of each species (Brown and Kurzius 1989). However, my study illustrates that in areas where environmental conditions permit coexistence, risk of predation from *O. leucogaster* may modify the behavior and population dynamics of other grassland rodents, at least on a relatively short time scale. These results add to a growing body of evidence of the complexity of trophic interactions and provide additional evidence of intraguild predation in natural communities (Polis et al. 1989) and for the role of species interactions as a determinant of rodent community structure.

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Table 4.1. Microhabitat variables measured along trails of *Peromyscus maniculatus*. Except for PCTBARE and PCTLSHR, all variables were measured at randomly-selected 1-m points within each 5-m segment of the path (n=10 points for 50-m paths).

Variable	Description
DISTSHR	distance from trail point to nearest large shrub ($\geq$ 0.3 m in height; m)
PCTLSHR	percent of trail points within 0.1-m of a large shrub (%)
NOLSHR	number of large shrubs within 1 m of trail point
SHRSPAC	mean of distance from nearest large shrub to its 3 nearest neighbors (m)
SHRAREA	area of nearest large shrub (m^2)
NOSSHR	number of small shrubs (< 0.3-m in height) within 1 m of trail point
PCTBARE	percentage of trail points on bare ground (%)
NOBURR	number of burrows within 1 m of trail point
NODSTRB	number of soil disturbances ($\geq$ 0.25 m^2 in area) of trail point
DISTDRB	distance from trail point to nearest soil disturbance (m)

Table 4.2. Eigenvectors resulting from principal components analysis (PCA) of microhabitat characteristics along powder trails of *Peromyscus maniculatus* tracked prior to removal of *Onychomys leucogaster* and at 4 and 7 weeks after the first removals. See Table 4.1 for abbreviations for microhabitat variables.

Variable	PC1	PC2	PC3	PC4
DISTSHR	0.434	0.077	-0.009	0.055
PCTLSHR	-0.434	-0.124	0.111	-0.068
NOLSHR	-0.440	-0.070	0.032	-0.086
SHRSPAC	0.445	0.033	0.052	-0.019
SHRAREA	-0.265	-0.241	0.111	0.352
NOSSHR	0.239	0.169	0.585	-0.293
PCTBARE	0.129	0.153	-0.084	0.831
NOBURR	0.112	0.244	-0.772	-0.263
NODSTRB	-0.177	0.669	0.107	-0.024
DISTDRB	0.236	-0.596	-0.121	-0.117
Eigenvalue	4.578	1.506	1.181	1.094
Proportion of variance explained	45.78	15.06	11.81	10.94

Table 4.3. Percentage composition by volume of items in the diet of *P. maniculatus* during the removal experiment. Values are means, with SE given in parentheses (n=4 sites per treatment). The arthropod category includes animal tissues that could not be identified and assigned to taxonomic groups.

Category	Pre-removal		Post 4 weeks		Post 7 weeks	
	Control	Removal	Control	Removal	Control	Removal
Arthropods	85.57 (4.01)	85.27 (1.62)	62.53 (7.08)	69.02 (7.91)	65.02 (10.80)	47.48 (11.50)
Coleoptera	30.78 (8.92)	23.97 (8.81)	13.26 (2.71)	18.93 (5.81)	4.08 (4.08)	7.95 (5.24)
Scarabeidae	13.42 (8.48)	11.99 (6.57)	0	6.36 (6.36)	0	0
Tenebrionidae	0.38 (0.38)	0	2.89 (1.70)	0	0	0
Carabidae	1.71 (1.17)	5.26 (2.32)	0	0	0	0
Orthoptera	12.90 (3.07)	17.94 (6.72)	14.96 (2.60)	12.51 (7.31)	0.36 (0.36)	6.37 (2.86)
Larvae[1]	24.64 (7.96)	22.67 (4.91)	7.97 (4.66)	10.20 (4.40)	0.82 (0.82)	9.24 (9.24)
Araneae	1.89 (1.44)	1.99 (1.99)	0.77 (0.77)	0.35 (0.35)	2.55 (2.55)	1.84 (1.57)
Vertebrate	0	0.42 (0.42)	0.99 (0.57)	1.91 (1.91)	0	0
Seeds	5.45 (0.76)	6.61 (3.07)	28.49 (4.88)	25.64 (7.82)	30.89 (9.11)	44.88 (12.06)
Plant tissues	6.16 (1.10)	7.87 (4.05)	7.76 (2.12)	4.52 (1.16)	4.10 (1.80)	7.64 (2.87)
Fungus	2.82 (2.44)	0.24 (0.24)	0	0	0	0

1 primarily Lepidoptera

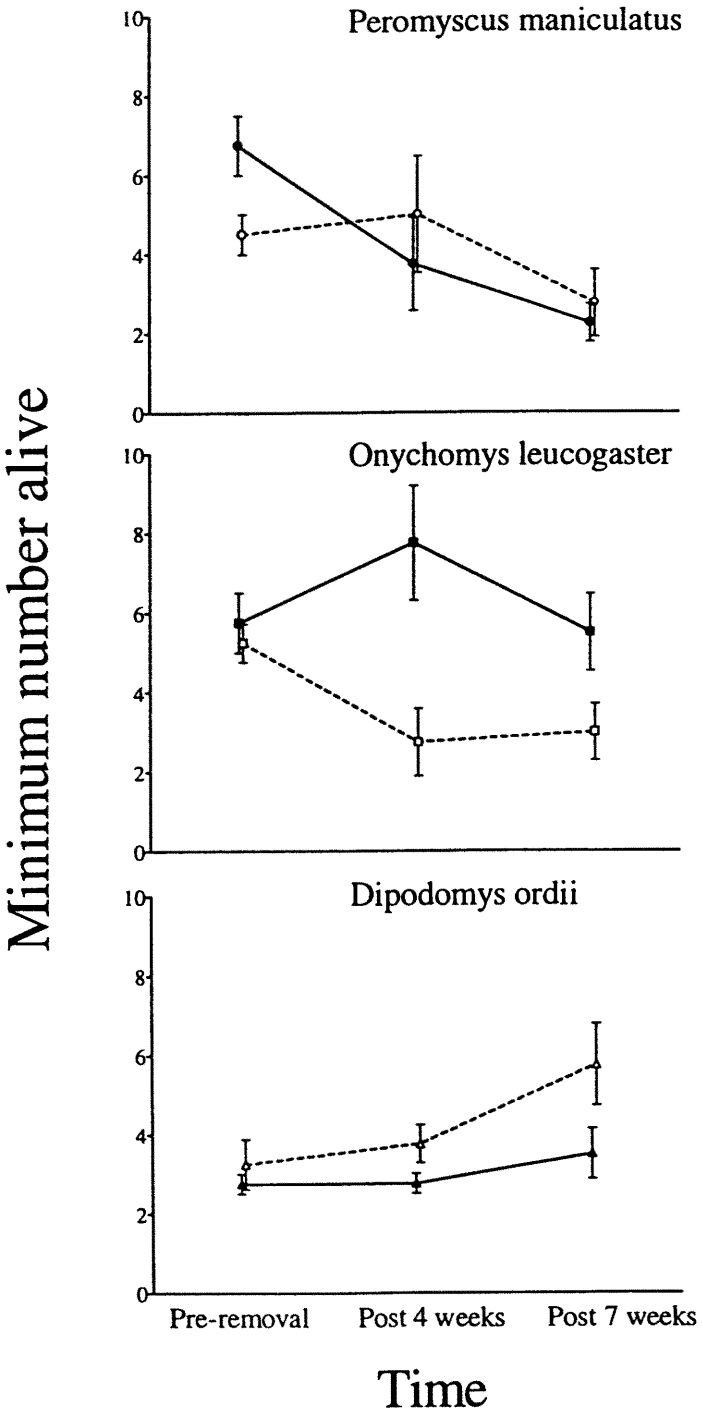

Fig. 4.1. Minimum number of *Peromyscus maniculatus*, *Onychomys leucogaster*, and *Dipodomys ordii* known to be alive on trapping webs prior to and at 4 and 7 weeks after initiating removals of *O. leucogaster*. Open symbols denote removal webs; closed symbols denote control webs. Values are means ± 1 SE (n=4 trapping webs per mean).

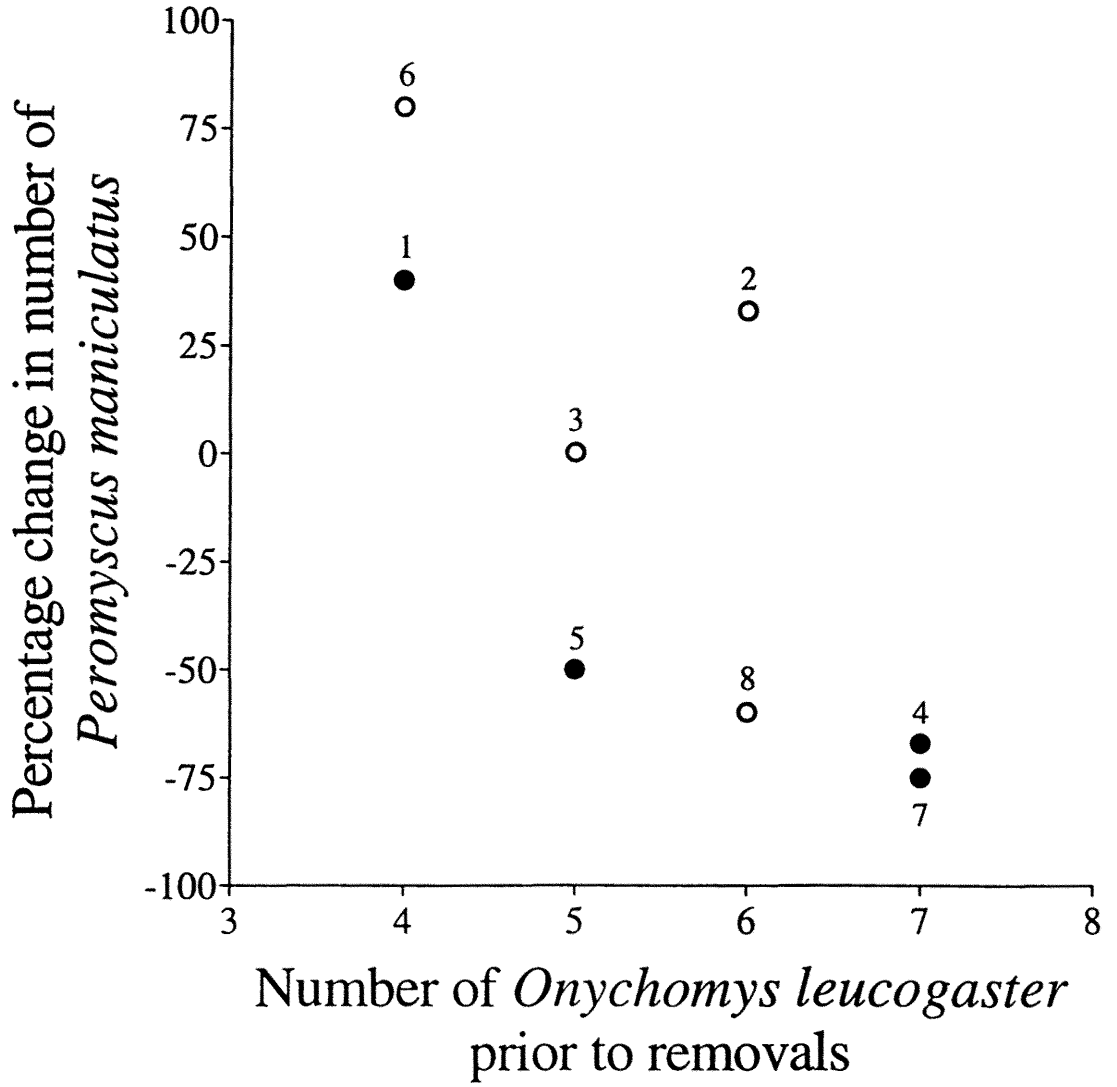

Fig. 4.2. Percentage change in number of *Peromyscus maniculatus* between pre-removal trapping and trapping conducted 4 weeks after first removals as a function of the number of *Onychomys leucogaster* present prior to removals. Open symbols denote removal webs; closed circles denote controls. The numerals above each value are the relative rank of shrub density of each site (1=highest density).

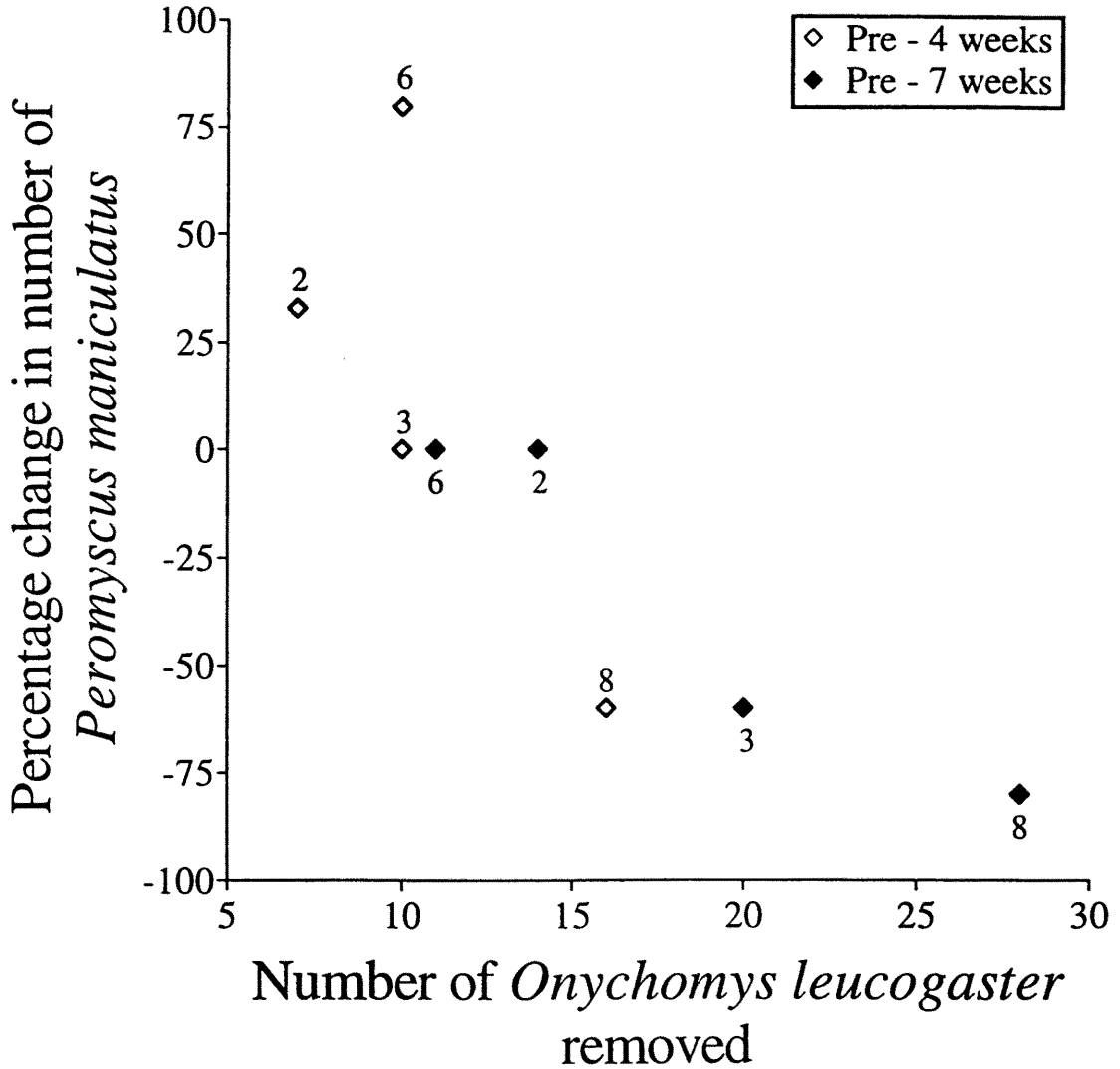

Fig. 4.3. Percentage change in number of *Peromyscus maniculatus* present on removal sites (n=4) between pre-removal trapping sessions and sessions conducted 4 weeks and 7 weeks after removal of the first *Onychomys leucogaster*. The number of *O. leucogaster* removed includes all individuals removed between and during post-removal sessions. The numerals associated with each value are the relative rank of shrub density of each site.

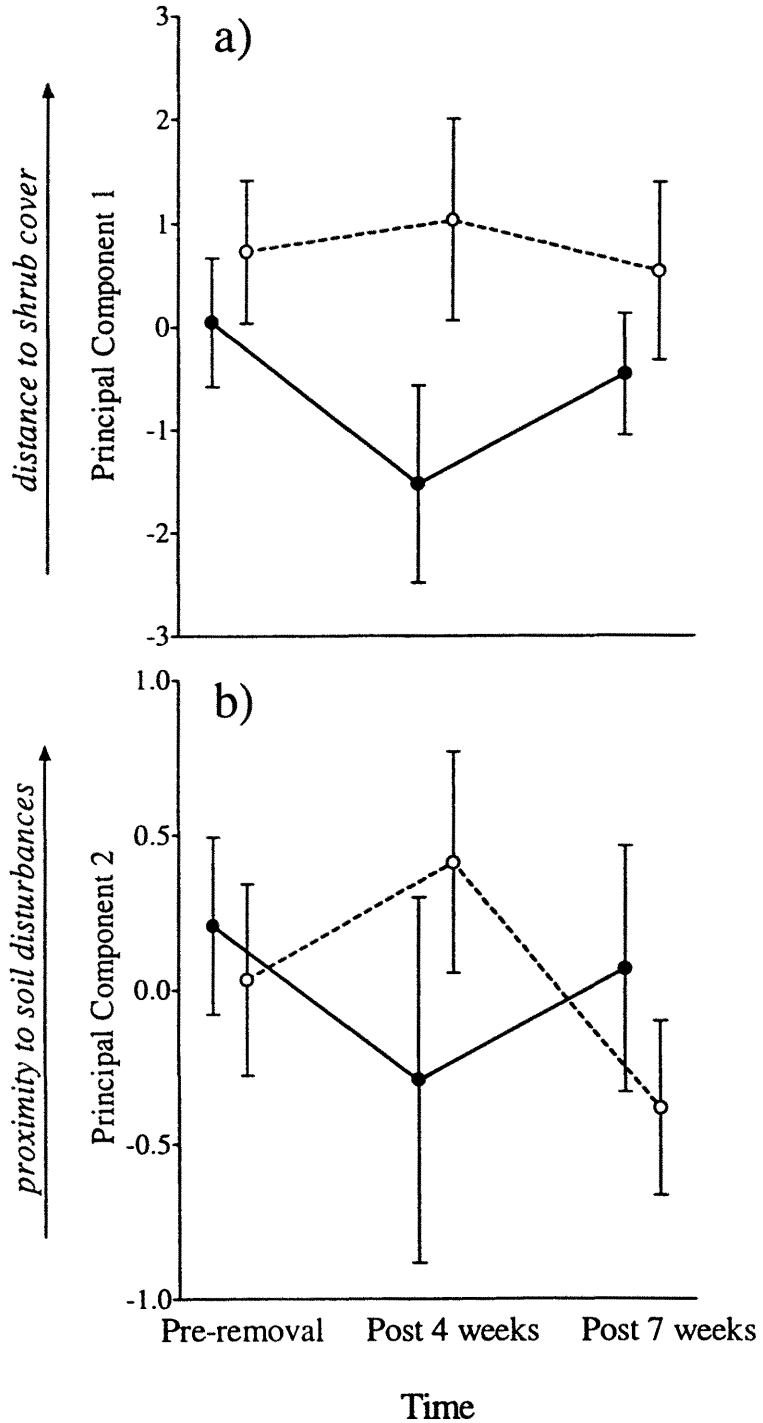

Fig. 4.4. Microhabitat use of *Peromyscus maniculatus* in response to removal of *Onychomys leucogaster*: a) Principal component 1, representing the use of shrub cover, and b) Principal component 2, depicting the use of soil disturbances. Values are means ± 1 SE (n=4 webs) of PCA scores calculated using transformed variables (see Table 4.1).

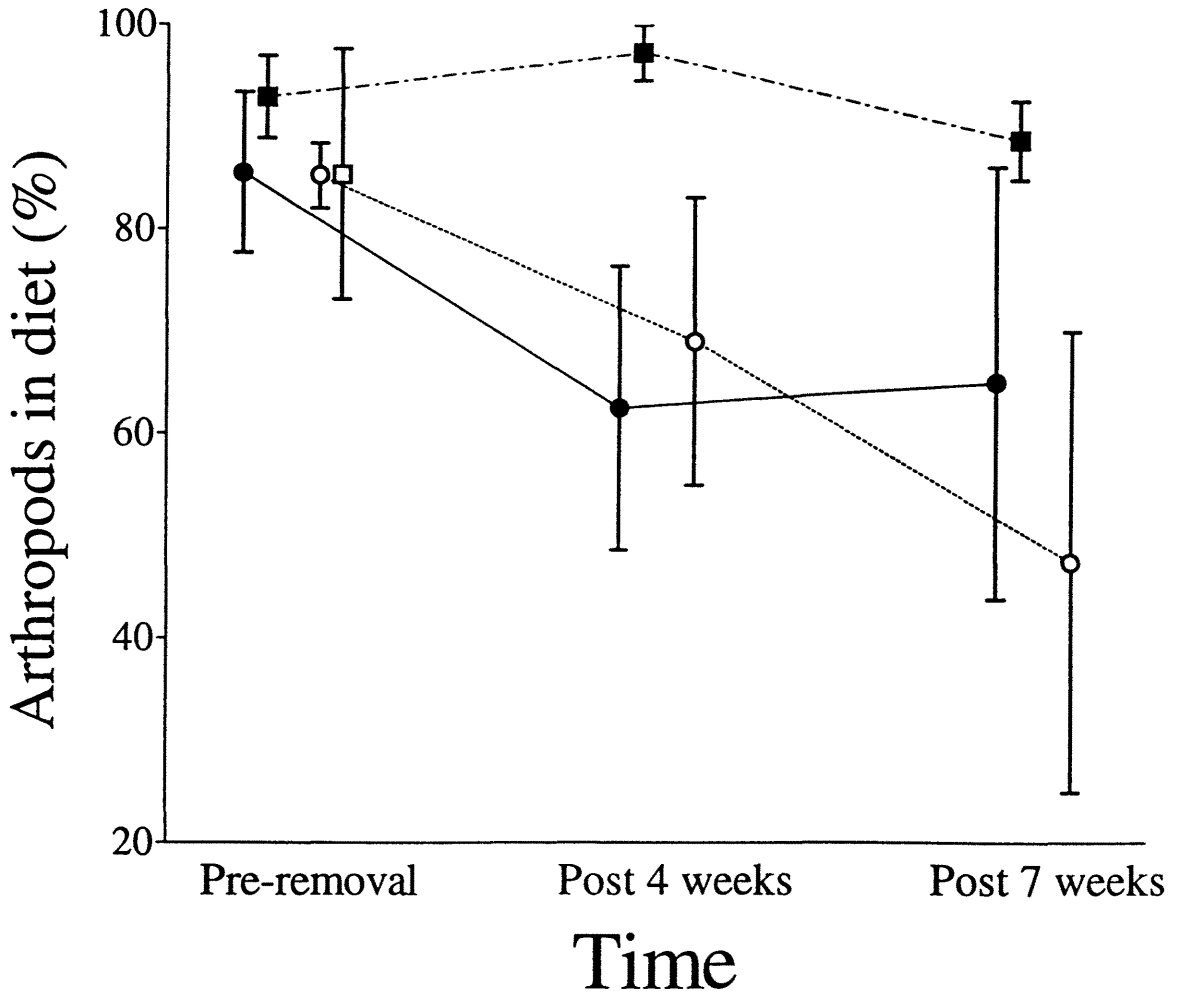

Fig. 4.5. Percentage of arthropods in the diet of *Peromyscus maniculatus* (circles) and *Onychomys leucogaster* (squares). Open symbols denote removal webs; closed symbols denote controls. Values are means ± 95% confidence intervals (n=8 mice of each species per treatment in each time period).

CHAPTER 5

DO OLFACTORY CUES MEDIATE INTERACTIONS BETWEEN RODENTS ON NORTHERN SHORTGRASS PRAIRIE?

ABSTRACT

I counted captures of free-ranging deer mice (*Peromyscus maniculatus*) in odor-baited traps to determine whether deer mice use olfactory cues to detect and evade grasshopper mice (*Onychomys leucogaster*), a predator and possible competitor on northern shortgrass prairie. Avoidance was measured using the frequency of captures in traps containing grasshopper-mouse odors compared to that in traps containing odors of an innocuous rodent (*Reithrodontomys megalotis*), and clean traps. I predicted that deer mice would be most deterred by odors in areas where grasshopper mice were common, and during winter, when alternative prey for grasshopper mice are less abundant. I also expected reproductive females to show greater avoidance because of the vulnerability of litters in burrows. Surprisingly, deer mice showed no evidence of avoidance in any experiments. These results are consistent with trapping records from capture-recapture studies on my site. I assert that grasshopper mice may affect the surface activity of deer mice, but that deer mice apparently do not use olfactory cues to avoid grasshopper mice. Taken with other studies noting the lack of avoidance of predator odors by deer mice and similar species, my results suggest that the response of rodents to predator odors is more variable than has been previously appreciated.

INTRODUCTION

Numerous studies have documented the importance of olfactory cues in mediating social and interspecific interactions of small mammals (Drickamer et al. 1992 and references therein). Many rodents use odor cues to detect and avoid both potential competitors (Daly et al. 1980, Drickamer et al. 1992) and mammalian predators (Madzer et al. 1976, Dickman 1992, Drickamer et al. 1992, Jędrzejewski et al. 1993, Nolte et al. 1994, Zimmerling and Sullivan 1994, and references therein). Such cues may be particularly useful for prey species because they allow individuals to recognize and evade predators without visual or direct contact, and because they may remain in an area for an extended period of time and provide information on the temporal status of a predator's activity.

The northern grasshopper mouse (*Onychomys leucogaster*) and deer mouse (*Peromyscus maniculatus*) are nocturnal murid rodents that inhabit desert and semi-arid grasslands of the western United States and southwestern Canada. Grasshopper mice are unusual compared to other North American rodents in being mostly arthropodivorous (McCarty 1978), and numerous studies suggest that they prey on other rodents, including deer mice (Bailey and Sperry 1929, Egoscue 1960, Horner et al. 1965, Ruffer 1968, Cole and Wolfe 1970, Flake 1971, Rebar and Conley 1983). In many regions, deer mice are omnivorous and consume many insects; this dietary overlap with grasshopper mice may therefore result in interspecific competition. Adult grasshopper mice are approximately 33% larger than adult deer mice (Armstrong 1972) and, as potential predators, their presence may influence the surface activity of deer mice. Rebar and Conley (1983) found that kangaroo rats (*Dipodomys ordii*) shifted microhabitat use in the presence of grasshopper mice, and it seems likely that grasshopper mice may have a similar or more significant impact on deer mice because of their greater similarity of size and ecology.

If grasshopper mice pose a threat to other small mammals, then one might expect rodents such as deer mice to be able to detect and avoid grasshopper mice prior to contact. Because deer mice may use odor cues in interactions between both conspecifics and other

rodents (Daly et al. 1980, Drickamer 1984), and because grasshopper mice possess a strong musky odor that may be deposited on the substrate in the form of urine, feces, and territorial signposts (Ruffer 1965), I predicted that avoidance could be effected through olfactory cues.

I compared the frequency of captures of deer mice in traps containing fecal and urinary odors of grasshopper mice or of western harvest mice (*Reithrodontomys megalotis*), as well as in clean traps to determine whether deer mice use olfactory cues to avoid grasshopper mice on shortgrass prairie. I focused largely on the behavior of deer mice because they co-occur with grasshopper mice on many prairie cover types, and because these two species frequently are the most abundant mice on my study area in north-central Colorado. Harvest mice are present in many areas of high population densities of deer mice, and were chosen to represent a rodent odor that was presumably innocuous. I tested four predictions:

1) Deer mice would be captured more frequently in traps containing harvest mouse odors or in clean traps than in traps containing odors of grasshopper mice.

2) Odors of grasshopper mice would be a greater deterrent to deer mice in areas where grasshopper mice are common than to mice living in areas where grasshopper mice are rare (i.e., avoidance is enhanced by prior experience and continued exposure).

3) Because females with litters in burrows probably are more vulnerable to predation by grasshopper mice, female deer mice, particularly those in reproductive condition, would be more likely to avoid traps containing grasshopper mouse odors.

4) Deer mice are more likely to be preyed upon by grasshopper mice during winter when the availability of preferred prey (arthropods) is reduced, and hence will show greater avoidance during winter than in summer.

METHODS

Study Area

My experiments were conducted from June to December 1993 on the Central Plains Experimental Range, located approximately 60 km northeast of Fort Collins, Colorado, USA

(40° 49' N latitude, 107° 47' W longitude). The climate is semi-arid: mean monthly temperatures range from -5° C in January to 22° C in July, and most of the 321 mm of annual precipitation falls in brief summer thunderstorms (Coffin and Lauenroth 1990). The topography consists of flat uplands separated by shallow swales and broad seasonal drainages. Upland vegetation is open grassland and is dominated by *Bouteloua gracilis*. Lowland areas typically contain an abundance of four-wing saltbush (*Atriplex canescens*) as well as a variety of small shrubs. The species diversity and population density of rodents are greater in lowland areas than in uplands (Chapter 6; Lindquist et al. 1995), although rodent biomass generally is lower on shortgrass prairie than other North American grasslands (Grant and Birney 1979). Densities of deer mice and grasshopper mice typically range from 1 to 4 individuals/ha and rarely exceed 6 individuals/ha.

Odor-response experiments

I conducted experiments in June and August 1993 to examine the response of deer mice to trap odors on a trapping area where grasshopper mice were rarely captured (mean ± SE = 0.1 ± 0.1 individuals /100 trap-nights, n = 5 trapping sessions of 500 - 720 trap-nights each), and on areas where grasshopper mice were relatively common (1.0 ± 0.3 individuals/100 trap-nights, n=5 sessions). To test the hypothesis of seasonal differences in avoidance, I repeated the experiment in December 1993 on the site without grasshopper mice (a widespread decline in the abundance of deer mice unfortunately resulted in few or no captures on sites with grasshopper mice in Winter 1993). Deer mice and harvest mice were relatively common on the site where grasshopper mice were absent (2.8 ± 0.2 and 2.1 ± 0.4 individuals/100 trap-nights, respectively, n = 5 sessions), which was located in an area with fine-textured soils, dense cover of large saltbush, and little exposed soil. The grasshopper-mouse site used for the June experiment was located on an area with widely-spaced saltbush, numerous small shrubs, and numerous soil disturbances. Because deer mice had become extremely rare on this location by August, for the second experiment the site without grasshopper mice was moved to a nearby area dominated by small soapweed (*Yucca glauca*)

and perennial bunchgrasses (e.g., *Stipa comata*). Grasshopper mice were captured in equal numbers on both sites, and the number of deer mice on the second grasshopper-mouse site was similar to that on the first of these sites in June. All areas (2.25-3.24 ha) had been trapped on a regular basis since 1992.

Sherman live traps (7.6 X 8.9 X 22.9 cm; folding) were used in all experiments. To remove any residual odors before experiments, all traps were disassembled, scrubbed clean with warm water and dishwashing soap, and rinsed in a mixture of warm water and baking soda. To obtain odors for traps, I collected soiled raw cotton and feces from traps in which grasshopper mice and harvest mice had been captured off-site. These materials were immediately placed in separate plastic storage bags and stored in a freezer (Drickamer et al. 1992). Clean cotton was placed in traps assigned to contain no rodent odors. All subsequent handling of cotton was conducted with latex gloves or through clean plastic bags. Like materials were combined, and I did not separate cotton by sex or age of the individuals captured. Traps were provided with the freshest materials available and unused materials were discarded after one month in the freezer.

At the beginning of each experiment, I baited traps with a small ball (ca. 5 g) of peanut butter and oats, which was wrapped in wax paper and hung from the back of the trap. This technique prevented loose bait from blocking treadles and causing trap malfunctioning and allowed me to detect traps that had been visited but not tripped. Traps were supplied with one of the three odors by placing a small piece (ca. 2.5 g) of cotton at the rear of the trap. I placed traps at grid stations where deer mice had been captured consistently during 4-5 recent nights of trapping. Each of the three contained a different odor and traps were placed 10-cm apart and faced inward in spoke-like fashion. The position of each trap was determined randomly prior to setting the traps. I set 20 trap-sets per grid in the June experiment, 13-15 per grid in August, and 11-15 in December. Traps were set for three consecutive nights during each experiment and sites were trapped concurrently.

I set traps at dusk and checked them at approximately 30-min intervals until 0100 h

and approximately hourly thereafter until dawn or whenever I heard traps close (to prevent multiple captures at a triad). When a mouse was captured, I replaced the trap with a fresh one with the same odor, checked the remaining traps for evidence of trap malfunction, and re-randomized the positions of the traps. I determined the age, sex, and reproductive status (males: obvious testes; females: evidence of pregnancy or lactation) of mice and held them in traps until they were released the following morning at the location of capture.

Odor preference was indicated by capture in a trap containing a particular odor cue. Captures of deer mice were included in analyses when only deer mice were captured at a station and when only a single trap was closed. I also included cases (14 captures) in which a mouse was captured in a trap and a second trap had evidence of occupancy (partially-eaten bait) but was not tripped; I assumed that the untripped trap had been entered first and therefore assigned captures from these sets to the odor of the untripped trap. I omitted instances in which one or more traps were empty and closed, or when multiple traps contained evidence of malfunction. I constructed linear logit models (Vepsäläinen and Savolainen 1988) using the CATMOD procedure of SAS (SAS Institute 1989) to test for the effects of presence/absence of grasshopper mice, sex, reproductive status, and season on the distribution of captures of deer mice among odor types. I also occasionally captured harvest mice and kangaroo rats (*D. ordii*), and used these captures to investigate whether these rodents exhibited any evidence of avoidance.

Capture-recapture studies

I searched for evidence of avoidance of grasshopper mice in trapping records from 30 mark-recapture trapping sessions conducted on the study area during 1992-1994. Trapping sessions consisted of 4-5 consecutive nights of live-trapping (228-720 TN per session) on sites where both deer mice and grasshopper mice were frequently captured. Traps contained cotton for bedding, and although feces and soiled cotton often were removed from traps, they were not cleaned, so recent fecal and urinary odors likely remained in traps following captures.

The relative infrequency of captures of deer mice and grasshopper mice at the same trap stations is suggestive of avoidance, but I adopted a more conservative criterion that allowed me to distinguish avoidance from differences in microhabitat use. I identified trap stations where individuals of both species were captured during the same trapping session as suitable microhabitat for either species. Avoidance was indicated by the lack of additional captures of deer mice at one of these stations following capture of a grasshopper mouse. Instances in which a deer mouse was captured at a station where a grasshopper mouse had been captured on an earlier night provided evidence against avoidance. I also compared captures of both species to those of kangaroo rats, a granivorous rodent whose presence presumably does not affect deer mice (but see Heske et al. 1994), but which may avoid grasshopper mice (Rebar and Conley 1983).

RESULTS

I captured 22 different deer mice in June (11 each on sites with and without grasshopper mice), 20 in August (7 and 13 on sites with and without grasshopper mice, respectively), and 13 on the site without grasshopper mice in December. Of the 107 captures used in my analyses, 41 were in traps containing odors of grasshopper mice, 38 were in traps containing harvest mouse odors, and 28 were in clean traps. Therefore, pooling all captures, there was no significant difference in the proportion of captures among odor types ($G = 2.69$, d.f. = 2, $P = 0.26$), and no evidence of avoidance of grasshopper mice. There was a tendency for mice to be more attracted to traps containing rodent odors than to clean traps ($G = 2.58$, d.f. = 1, $P = 0.10$), but this pattern was not consistent on all sites in all experiments (Fig. 5.1).

Considering only summer experiments, there were no significant differences in the distribution of captures between areas where grasshopper mice were common and where they were rare ($X^2 = 1.89$, d.f. = 2, $P = 0.39$), nor were there differences between the distribution of captures between sites for the June and August experiments ($X^2 = 2.04$, d.f. = 2, $P = 0.36$; Fig. 5.1). There was no evidence that deer mice on the site without grasshopper mice were more likely to avoid grasshopper mice during winter ($X^2 = 0.11$, d.f. = 2, $P = 0.95$); this

result did not change if summer experiments on both type of sites were included ($X^2 = 0.29$, d.f. = 2, P = 0.87).

Overall, more male mice than females were captured, but the odor preferences did not differ between sexes ($X^2 = 0.60$, d.f. = 2, P = 0.74). Further, reproductive females were no more likely to avoid odors of grasshopper mice than were other mice ($X^2 = 0.86$, d.f. = 2, P = 0.65), regardless of whether or not they were in areas where grasshopper mice were abundant ($X^2 = 0.56$, d.f. = 2, P = 0.76). Captures from the December experiment were not included in these analyses because no mice in reproductive condition were captured at that time.

Capture-recapture records from studies on the Central Plains Experimental Range also failed to show any evidence of avoidance by deer mice of residual odors left in traps by grasshopper mice, although captures of different species at the same station during a trapping session were relatively uncommon (Table 5.1). Deer mice seemed to respond similarly to traps previously catching grasshopper mice and kangaroo rats, in that most captures at the same location provided no evidence of avoidance. Kangaroo rats and grasshopper mice were more frequently captured at the same stations, perhaps reflecting similarities in their microhabitat affinities, and there was a tendency for kangaroo rats to be deterred by traps in which grasshopper mice had been captured (Table 5.1). Incidental captures of kangaroo rats during odor response experiments (Fig. 5.2), however, did not support this pattern. Harvest mice were captured less frequently in traps containing odors of grasshopper mice than in clean traps or in traps with harvest-mouse odors (G = 2.54, d.f. = 1, P = 0.10; Fig. 5.2), which suggests that they were capable of avoiding grasshopper mice using the cues provided.

DISCUSSION

Although grasshopper mice have been hypothesized to function as predators and competitors of deer mice on shortgrass prairie, I found no evidence in my odor-response experiments that deer mice avoid grasshopper mice using olfactory cues. An analysis of trapping records from my mark-recapture studies supports this conclusion. The discriminatory abilities of deer mice may be such that mice could assess the age of the odors I

provided, and therefore concluded that the grasshopper mouse odors were old and represented no threat. My methods, however, were similar to those used in other studies that have demonstrated that rodents discriminate among and respond to odors in live traps (e.g., Daly et al. 1980, Dickman and Doncaster 1984, Stoddart and Smith 1986, Drickamer et al. 1992). Furthermore, results from an unpublished pilot study indicated that deer mice responded to the volatile cues I provided in traps. Incidental captures of harvest mice (Fig. 5.2) also suggest that they avoided grasshopper mice or were attracted to odors of conspecifics based on the odor cues provided, so my odor-baiting technique presumably was effective. I was not surprised that harvest mice showed evidence of avoidance; this species is approximately one-third the size of grasshopper mice and was most abundant on areas of shortgrass prairie when and where grasshopper mice were uncommon.

Contrary to my predictions, the response of deer mice to grasshopper mouse odors in traps was not influenced by previous exposure to grasshopper mice. In a similar study, Dickman (1992) reported that house mice (*Mus domesticus*) did not discriminate predator odors in areas without mammalian carnivores, but avoided these odors where predators were present. Mice may be more likely to avoid odors of those predators that they encounter most frequently or that pose the most significant threat (Madzer et al. 1976; Dickman 1992; Jędrzejewski et al. 1993). Others (Stoddart 1980, 1983; Dickman and Doncaster 1984), however, have suggested that the feces, urine, or anal-gland secretions of mammalian carnivores contain similar chemical cues that trigger avoidance by rodents, regardless of their ecological overlap or history of contact. Despite differences in the distribution of grasshopper mice among cover types of shortgrass prairie, over time there may be sufficient contact between deer mice and grasshopper mice to prevent deer mice on sites without grasshopper mice from having lost their ability to detect grasshopper mouse odors. This phenomenon, however, would not explain the apparent lack of avoidance on all sites.

It is possible that deer mice rarely encounter or are indifferent to the activity of grasshopper mice, so that there has been little selective pressure on the behavior of deer mice

to avoid grasshopper mice. Some reports of predation by grasshopper mice on deer mice and other rodents are from laboratory studies (Egoscue 1960; Ruffer 1968; Cole and Wolfe 1970), but predation evidently occurs under natural conditions. Flake (1971) reported that mammalian hair and tissue (including deer mice and kangaroo rats) accounted for 9-10% of the animal remains in the diet of grasshopper mice on my study area. Bailey and Sperry (1929) found the remains of deer mice, harvest mice, kangaroo rats, pocket mice (*Perognathus* sp.), and voles (*Microtus* sp.) in stomachs of field-caught grasshopper mice and concluded that small mammals may constitute 2-6% of the foods eaten. It is difficult to assess the importance of natural predation by grasshopper mice because predation has rarely been observed directly (but see Rebar and Conley 1983) and because grasshopper mice may selectively consume individuals or portions of prey that may not be readily identified in diet studies. For example, predation on nestling mice in burrows, such as that reported by Getz et al. (1992) for short-tailed shrews (*Blarina brevicauda*) on meadow voles (*M. pennsylvanicus*), may be difficult to detect because nestlings have little hair (Horner et al. 1965). Thus, even if attacks on adult mice were relatively infrequent, predation on litters could negatively impact deer-mouse populations. In addition, results from a separate study (Chapter 4) suggested that deer mice shift microhabitat use to avoid grasshopper mice, so it may be premature to conclude that interactions between these species are unimportant based solely on the results of my odor-response experiment.

An alternative explanation is that deer mice either cannot distinguish odors of other rodents, or that they do not use olfactory cues in interspecific interactions. Deer mice use odor cues to identify and assess the reproductive condition of conspecifics (Gurnell and Little 1992 and references therein), but they may not distinguish between heterospecific and neutral odors (Wuensch 1982). Daly et al. (1980) stated that deer mice differentiated between clean traps and those containing odors of reputed competitors (kangaroo rats), but they found evidence of avoidance only when the mouse's reproductive status was considered and only for the smaller of the two competitors studied. It is not clear, however, why reproductive status

should affect a mouse's ability to detect odors of competitors, or why only reproductive mice would be attracted to these odors (Daly et al. 1980).

Given the carnivorous habits of grasshopper mice, my results support those from other researchers who have noted the lack of response of *Peromyscus* to predator odors in field experiments. Sullivan et al. (1988a) noted that deer mice entered traps containing odors of stoats (*Mustela erminea*) and red foxes (*Vulpes vulpes*), although mice were not provided with a choice of odors and may have been attracted to baited traps. Madzer et al. (1976) similarly found that *P. leucopus* readily entered traps containing weasel feces (*M. frenata*). The application of mustelid semiochemicals to forest plantations in British Columbia had no significant effect on deer-mouse populations (Zimmerling and Sullivan 1994).

In spite of this evidence, I cannot satisfactorily explain why olfactorally-mediated predator avoidance would not be advantageous for deer mice, particularly when it apparently is employed by many other rodents. However, Old World wood mice (*Apodemus* sp.) also apparently do not differentiate between heterospecific and neutral odors (Stoddart and Smith 1984, 1986; Gurnell and Little 1992) and do not avoid traps containing predator odors (Stoddart 1976, 1980, 1983; Dickman and Doncaster 1984; Gorman 1984; Little 1985, cited in Robinson 1990; but see Robinson 1990). *Peromyscus* and *Apodemus* are similar in morphology, behavior, and life-history traits, and are often considered to be ecologically equivalent, at least in a broad sense (Montgomery 1989). Species of both genera typically exhibit moderate seasonal changes in abundance and are preyed upon by similar mammalian and avian predators (Montgomery 1989; Terman 1993). It is not clear, however, that predators are responsible for fluctuations in population size of *Peromyscus* and *Apodemus*, at least to the degree suggested for other rodents whose populations exhibit multi-annual cycles (*Microtus* sp.: Henttonen et al. 1987, Erlinge 1987) or episodic irruptions (*Mus* sp.: Sinclair et al. 1990). Avoidance of predator odors is well-documented in these latter groups (Sullivan et al. 1988a; Merkens et al. 1991; Dickman 1992; Drickamer et al. 1992; and references therein; but see Boonstra et al. 1982).

I speculate that differences in the odor responses of *Peromyscus* and *Apodemus* compared to other rodents may reflect an interaction between the behavior of some predators and prey population dynamics. For example, if mammalian predators responded to high prey densities or preferred species with the potential to reach high numbers, then selection should favor strongly individuals of these taxa that are alerted by and avoid predator cues. The evolution of odor avoidance could be enhanced in cyclic or irruptive rodents if, as suggested by Jędrzejewski et al. (1993), the hunting success of predators declined with increasing prey abundance (Vermeij 1982). For individuals in relatively sparse or stable populations, encounters with predators and predator cues may be relatively infrequent or predator success rates may be high, so that there are few opportunities to associate successfully the threat of predation with olfactory cues and little difference in fitness between those individuals that react to predator odors and those that do not. For example, predator odors may not be useful to either *Peromyscus* or *Apodemus* in winter, when both may enter torpor (Jędrzejewski et al. 1992).

This scenario assumes that there is heritable variation in the response of individuals to olfactory cues, that individuals wary of predator odors contribute more to future generations than those that are not, and that predator success is usually negatively correlated with prey abundance. My model may not be adequate to explain the avoidance of predator odors by other rodents (e.g., *Thomomys talpoides*, Sullivan et al. 1988b; *Marmota monax*, Swihart 1991; *Aplodontia rufa*, Epple et al. 1993) and alternative explanations may be equally plausible. It is apparent, however, that all rodents do not respond to predator odors in the same fashion, and additional studies are needed to clarify the use of heterospecific odors by *Peromyscus* and *Apodemus* and to identify the mechanisms responsible for the evolution of odor avoidance as an antipredator strategy.

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Table 5.1. Evidence of avoidance of residual trap odors from capture-recapture studies on the Central Plains Experimental Range in north-central Colorado. Results summarize captures from 30 trapping sessions of 4-5 nights each (ca. 10,400 trap-nights) during 1992-1994 on areas where deer mice (*Peromyscus maniculatus*), grasshopper mice (*Onychomys leucogaster*), and kangaroo rats (*Dipodomys ordii*) were captured regularly. Numbers in parentheses indicate total numbers of captures of each species. The number of captures at the same station describes the number of captures of species 1 and species 2 at the same trap station during a given trapping session. After a capture of species 1 at a given trap station, species 1 avoided species 2 if, after a capture of species 2, there were no additional captures of species 1 at that station. Lack of avoidance was indicated by capture of species 1 at a trap station after capture of species 2 at that station on an earlier night. Values for avoidance and lack of avoidance do not sum to the numbers of captures in common because some captures could not be classified.

Species 1 vs. Species 2	Number of captures at the same station	Avoidance	No Avoidance
Deer mice (317) vs. grasshopper mice (470)	28	4	15
Deer mice (317) vs. kangaroo rats (276)	20	5	10
Kangaroo rats (276) vs. grasshopper mice (470)	33	12	9

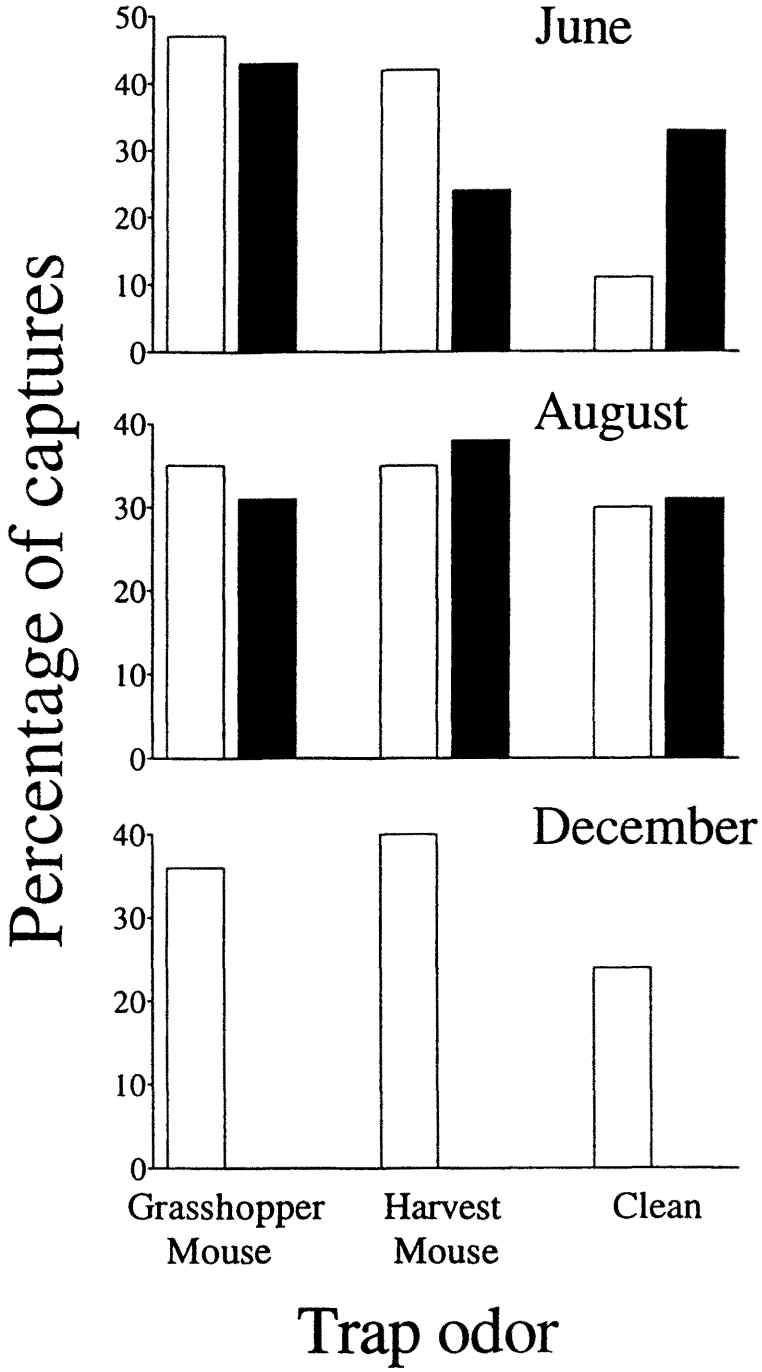

Fig. 5.1. Percentage of captures of deer mice (*Peromyscus maniculatus*) in traps containing odors of northern grasshopper mice (*Onychomys leucogaster*) and western harvest mice (*Reithrodontomys megalotis*), and traps with no odors in experiments conducted in June, August, and December 1993 on the Central Plains Experimental Range. Open bars denote experiments where grasshopper mice were extremely rare (n = 19 and 26 captures for June and August, respectively), whereas dark bars denote experiments where grasshopper mice were abundant (n = 21, 16 and 25 captures for June, August, and December, respectively).

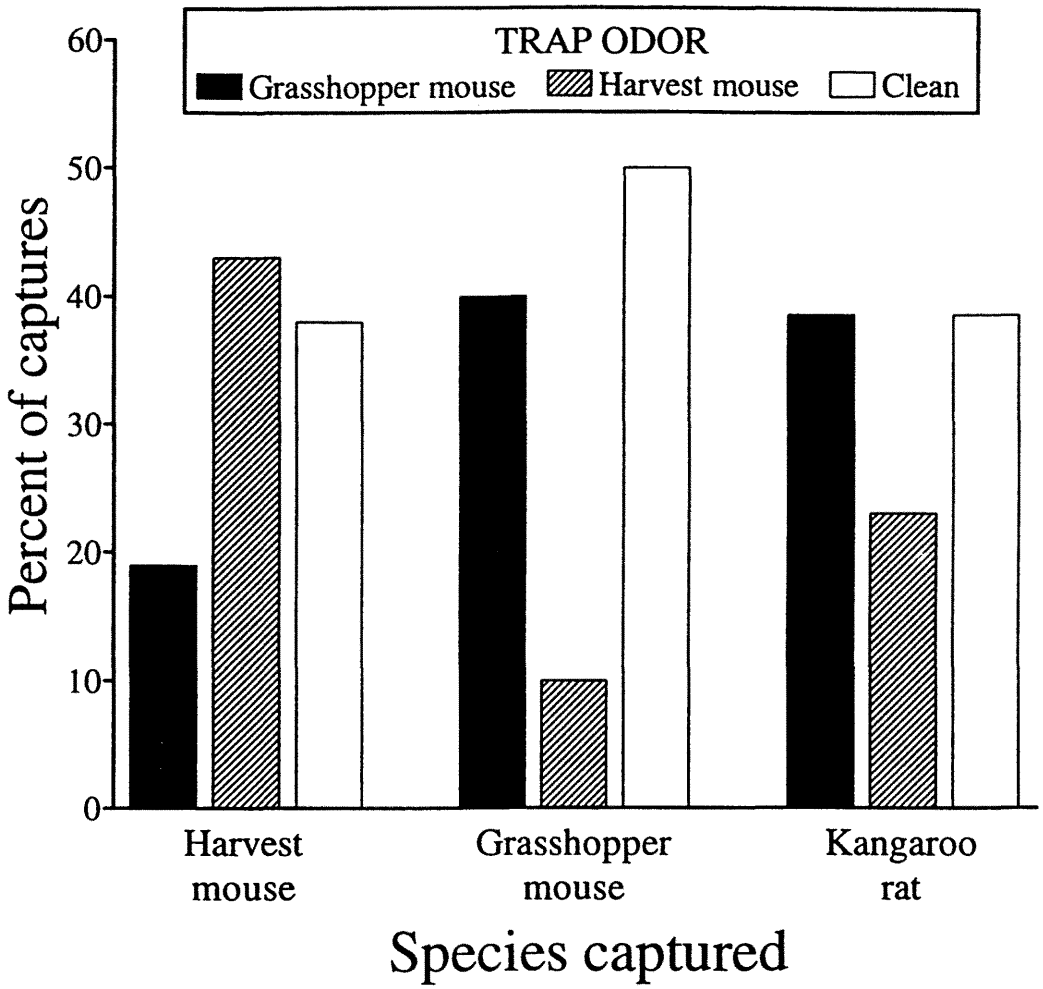

Fig. 5.2. Percentage of captures of western harvest mice (*Reithrodontomys megalotis;* n = 26 captures), northern grasshopper mice (*Onychomys leucogaster;* n = 10 captures), and Ord's kangaroo rats (*Dipodomys ordii;* n = 13 captures) in traps containing odors of northern grasshopper mice (dark bars) and western harvest mice (hatched bars), and traps with no odors (empty bars). Results are incidental captures from three odor response experiments conducted in 1993 on the Central Plains Experimental Range.

CHAPTER 6

MONITORING STUDIES OF SMALL-MAMMAL POPULATIONS ON THE SHORTGRASS STEPPE LONG-TERM ECOLOGICAL RESEARCH SITE

ABSTRACT

Long-term studies are necessary to track changes in population and community dynamics of small mammals (rodents and lagomorphs) in shortgrass steppe. In 1994, I established sampling protocols based on distance-sampling procedures to monitor small-mammal populations across representative shortgrass-steppe cover types in north-central Colorado. These data will serve as baseline information for other studies conducted on the Central Plains Experimental Range and will allow comparative studies among other sites in the Long-Term Ecological Research project network. Densities of nocturnal rodents are estimated in late-spring and late-summer by live-trapping on three grassland and three saltbush-dominated trapping webs. Populations of lagomorphs are surveyed by driving a permanent transect on one night in each season. My first year of results revealed that both density and species diversity of rodents was higher on saltbush areas than on grasslands. Eight rodent species have been captured to date, but three species (*Onychomys leucogaster*, *Peromyscus maniculatus*, and *Dipodomys ordii*) comprise more than 90% of individuals captured. Three species of lagomorphs are present on the study area (*Sylvilagus audubonii*, *Lepus californicus*, *L. townsendii*). *L. townsendii* are extremely rare, whereas densities of the other species appear to fluctuate seasonally. Additional long-term studies focused on other vertebrate groups (ground squirrels, pocket gophers, herptofauna) are needed to monitor representative consumer populations effectively.

INTRODUCTION

Small mammals such as rodents and lagomorphs influence the structure and function of grassland ecosystems as consumers of plants and arthropods, as movers of soil and soil nutrients, and as the primary prey of raptors and carnivorous mammals (Grant and French 1980). Because of their intermediate trophic position and potential for dispersal, populations of small mammals may track changes in vegetation and the abiotic environment that result from shifts in land-use practices and other anthropogenic disturbances. However, these populations are variable over space and time, and their response to environmental changes may not be immediately apparent given their behavioral flexibility and relatively long life-spans and generation times. Long-term studies of population and community dynamics therefore are needed to fully understand the role of small mammals in grassland ecosystems.

One of the central missions on the Long-Term Ecological Research (LTER) program is to document the spatial and temporal distributions of populations representative of trophic structure (Callahan 1984). Direct consumption of primary production by small mammals is a relatively small component of energy flow through the semiarid shortgrass-steppe region of the Central Plains (Grant and French 1980), but these animals may have significant effects on populations of other consumers such as arthropods or may influence vegetation structure directly, e.g., through the consumption of mid-grasses and shrubs (Lauenroth and Milchunas 1991) or indirectly, through seed predation (Hoffman et al. 1995). Furthermore, the movement of soil and soil nutrients by fossorial and semi-fossorial rodents may influence vegetation diversity, soil hydrology, and the abundance of other consumers (Grant and French 1980, Huntly and Inouye 1988). Small mammals are also sensitive to changes in vegetation structure and resource availability caused by manipulations of productivity (Abramsky et al. 1979, Hall and Willig 1994) and grazing (Grant et al. 1982). Patterns in the distribution and abundance of small mammals, thus, may simultaneously reflect and affect the stability of shortgrass-steppe ecosystem. Understanding the role of small mammals in ecosystem structure and function is particularly important because of the historical and current

exploitation of prairie landscapes by agricultural practices and the impacts on the native mammalian fauna.

In conjunction with the Shortgrass Steppe LTER project, I established sampling protocols in 1994 to monitor populations of nocturnal rodents and lagomorphs on shortgrass steppe in north-central Colorado. My objectives were to: 1) assess spatial and temporal patterns of abundance and community composition of small mammals among representative cover types of northern shortgrass steppe; 2) provide baseline information to aid future small-mammal and ecosystem-level studies on the site; and 3) establish a long-term database that could be used in comparative studies of the dynamics of small mammal populations among other sites in the LTER network. Protocols were designed with the assistance of R. Parmenter at the Sevilleta Wildlife Refuge LTER site and were similar to monitoring procedures in place at the Sevilleta and Jornada LTER sites. The assistance of M. Lindquist, the site manager for the Shortgrass Steppe LTER project, was instrumental in the implementation of field studies. Here, I describe data collection and analysis procedures and discuss preliminary patterns based on the first year of results.

METHODS

Study area

The Shortgrass Steppe LTER site is located in north-central Colorado at the Central Plains Experimental Range (CPER), approximately 60 km northeast of Fort Collins. The United States Department of Agriculture Agricultural Research Service administers the CPER, which was established in 1939 to study the effects of cattle grazing on rangelands. From 1968 to 1976, western portions of the 6200-ha site represented shortgrass prairie (Pawnee site) in the Grassland Biome of the United States/International Biological Program (US/IBP). Research through the LTER project began in 1982 and is directed by I.C. Burke and W.K. Lauenroth at Colorado State University.

Two broad classes of vegetation can be distinguished on the CPER on the basis of shrub cover. On upland prairie sites, soils are sandy loam and the vegetation is low in stature

and dominated by two perennial shortgrasses (*Bouteloua gracilis* and *Buchloe dactyloides*). Plains prickly-pear (*Opuntia polycantha*), half-shrubs (*Artemisia frigida, Eriogonum effusum, Gutierrezia sarothrae, Ceratoides lanata, Chrysothamnus nauseosus*) and forbs (*Sphaeralcea coccinea*) are also present. In low-lying areas adjacent to ephemeral washes, soils tend to be more coarsely-textured, and four-wing saltbush (*Atriplex canescens*), small shrubs and a variety of mid-grasses (*Pascopyron smithii, Stipa comata, Aristida longiseta, Sitanion hystrix*) are common. Uplands are grazed by cattle in summer and fall, whereas most shrub-dominated areas are grazed in winter and spring. Other less common vegetation types include saltbush floodplain, a narrow (0.8-km wide) band of dense saltbush and *P. smithii* on loamy soils between Owl and Cow creeks; yucca prairie, areas of sandy or shale soils where small soapweed (*Yucca glauca*) is abundant; and riparian vegetation, represented by a stand of cottonwoods (*Populus sargentii*) and willows (*Salix* spp.) along Owl Creek in the northern portion of the study area.

Nocturnal rodents

Current monitoring efforts focus on nine nocturnal species that are commonly captured in large (7.6 x 8.9 x 22.9 cm) Sherman live traps (H.B. Sherman Traps, Inc., Talahassee, FL) (Appendix 1). Six 3.14-ha trapping webs were established in 1994, with three replicate webs on grasslands with Avar-Manzanola sandy-loam soils and three replicates on saltbush-dominated lowlands with Remmit loamy-sand soils. Trapping webs consisted of 124 live traps spaced 10 m apart in 12 transects radiating from a central point in a spoke-like fashion (Fig. 6.1). Traps were baited with a small ball of peanut butter and oats, wrapped in wax paper and hung in the rear of the trap, and a small amount of the mixture was sprinkled on the open door of the trap. Cotton was placed in the trap to reduce trap mortalities resulting from cold exposure.

To track populations over time, densities are estimated during two trapping sessions each year, one in August/ September and another in April/ May. The objectives of these studies are to obtain consistent approximate densities of small mammals at or immediately

prior to spring breeding (and overwinter survival of adults) and after the completion of most summer reproduction. Here, I present estimated densities from trapping sessions in September 1994, April/ May 1995, and September 1995. Sessions consisted of 4 consecutive nights of trapping during the dark phase of the lunar cycle, with three webs trapped concurrently. Traps were set in the early evening and checked and closed at dawn. Traps were set and checked with the assistance of the LTER field crew, usually working in pairs. Field assistants were trained and provided with gloves and HEPA-filter masks to minimize exposure to hantavirus and traps were handled and cleaned following precautions described in Mills et al. (1995). Traps could be set in <2 h, but checking and processing animals required 2-3 h each morning.

During morning checks, we recorded the trap number and the species, age, sex, and reproductive condition of all captured individuals. For first-time captures, individuals were weighed and marked on the throat and chest with a colored felt-tipped marker. These marks generally remained on animals for 3-5 d and allowed me to distinguish recaptures from new individuals. Unique marks for individuals (e.g., ear tags, PIT tags) are not used in our current studies because of the additional training and record-keeping required, so it is not possible to estimate recapture probabilities or monitor seasonal changes in habitat use or survival from our data. However, future researchers interested in studying population dynamics more intensively can trap more frequently on the premanent webs and give individuals unique marks in conjuction with our monitoring studies.

A preliminary survey of vegetation on webs was conducted in July 1995. Percent canopy cover was recorded in 0.2-m^2 point frame at 10-m intervals along four random 50-m transects on each web. Maximum height of saltbush and other vegetation were measured at each point frame. Percent cover of saltbush was also recorded along each transect using line-intercept methods (Hays et al. 1981). Burrow densities were estimated by counting the number of burrows within a 3-m radius of the point-frame locations. Only burrows $\geq$ 3 cm in diameter were recorded.

Lagomorphs

Population densities of the three resident species of lagomorphs (Appendix 1) are estimated by counting individuals spotted along a 32-km route within and along the periphery of the CPER (Fig. 6.2). The route is driven on one night during the dark phase of the lunar cycle in January, April, July, and October. For the present study, I estimated densities from July 1994 to July 1995 sampling periods.

Beginning at dark (i.e., no remaining sunlight in sky), the route was driven at a slow speed (8-16 km/h) in a four-wheel-drive pick-up, with two spotlighters and one observer in the bed of the truck. We recorded the perpendicular distance (to nearest 0.5 m) from the truck bed to the first known position of all lagomorphs sighted. During measurement of distances, one observer monitored the position of the sighted individual(s) to avoid counting rabbits more than once. The distance along the route (odometer reading), lagomorph species, and the number of individuals at the location (i.e., within ca. 1 m of each other). Counts required between 3-5 h to complete.

Density estimation

Population densities were estimated using distance sampling procedures in Program DISTANCE (Buckland et al. 1993). This modeling technique is useful for monitoring studies because it allows direct estimation of density (versus separate estimation of population size and sampling area) and allows for the use of batch rather than individual identification marks. Additionally, unlike finite sampling methods, distance sampling does not require detection of all individuals within an area. Trapping webs and transects also are easy to install and run, and a single modelling approach can be used for estimating densities of both lagomorphs and rodents.

Distance sampling uses the distances from a fixed random point or transect to individual or groups of objects (organisms) to model the probability of detecting an object, given its distance from the point or line (Buckland et al. 1993). Maximum likelihood procedures are used to evaluate model fit and to compare competing models. A final model is

used to estimate the area over which objects were detected, and thus provides an estimate of density. Distance sampling assumes that: 1) all objects on the transect or point are detected; 2) all objects are detected at their initial location (prior to movement); 3) distances are measured correctly; and 4) individuals are identified correctly.

Data from trapping webs were analyzed as point counts, with individuals detected by live-trapping within a band at a fixed radius from the web center. Only first-time captures of rodents were used in analyses. I estimated density separately for species for which I captured ≥15 individuals. If I captured <15 individuals of a given species, densities were estimated for all species combined. The density of a given species was then calculated by dividing the total density by the proportional representation of that species in the sample. If I captured <15 individuals of all species combined, then density was estimated by dividing the number of individuals captured of each species by the effective trapping area (4.52 ha). The effective trapping was the area bounded by the web, plus a 20-m boundary ring which was estimated from previous mark-recapture studies on the site (P. Stapp, unpublished data). The 32-km spotlighting route was treated as a single transect to estimate lagomorph densities. If <15 lagomorphs were seen, then density was calculated by dividing the number of each species detected by effective transect area (3.2 km^2; 50-m strip on each side of the 32-km transect).

RESULTS AND DISCUSSION

Nocturnal rodents

The vegetation on trapping webs differed primarily in the amount of four-wing saltbush ($P \leq 0.05$; Table 6.1). Saltbush webs had significantly more canopy cover of these shrubs, significantly less bare ground, and more burrows than grassland webs (Table 6.1). For most variables, however, there were no significant differences between vegetation types.

Overall, rodent densities on saltbush webs were 8-16 times higher than on grasslands (Fig. 6.3). More than 90% of all individuals captured were of three species (deer mouse, *Peromyscus maniculatus*; northern grasshopper mice, *Onychomys leucogaster*; Ord's kangaroo rat, *Dipodomys ordii*); most individuals captured were deer mice (36%) or

grasshopper mice (36%). Species diversity was consistently higher on saltbush webs, although two species were captured only on grasslands in September 1994 (Fig. 6.3). Only grasshopper mice and diurnal thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) were captured consistently on grassland webs. Because we closed traps shortly after dawn, we could not accurately estimate ground-squirrel abundance. However, diurnal trapping conducted in June and July 1995 revealed that ground-squirrel densities were approximately four times higher on saltbush webs than on grasslands (2.61±0.99 vs. 0.61±0.18 individuals/ ha, respectively; L. Higgins and P. Stapp, unpublished data.).

Differences in rodent density and diversity reflect differences in soil texture and in the structural complexity and diversity of vegetation. Two species that were relatively common on shrub-dominated areas were absent on grassland webs. *Dipodomys ordii* is granivorous and may respond to the abundance of seed-producing cool-season grasses and shrubs, or to the diversity of annual forbs associated with disturbed areas [e.g., pocket-gopher (*Thomomys talpoides*) mounds], that occur on more coarsely-textured soils. Seeds may also be more accessible where soils are more friable. Western harvest mice (*Reithrodontomys megalotis*) were most abundant in areas with large shrubs and tall, weedy vegetation. Abramsky et al. (1979), for example, documented colonization by *R. megalotis* of plots where vegetative cover had increased dramatically in response to water and nitrogen addition. Abramsky et al. (1979) considered *R. megalotis* to be an "exotic"species on shortgrass prairie, but this species can be relatively abundant in floodplain areas with dense *P. smithii*, *Kochia scoparia* and large saltbush (Appendix 2).

Other rodent species have been captured during other studies on the site but to date have not been captured during monitoring efforts (Appendix 2). Prairie voles (*Microtus ochrogaster*) prefer relatively dense grass and litter cover and weedy vegetation (Abramsky et al. 1979, Birney et al. 1976) and were usually found in association with *R. megalotis*. Voles may eventually be captured on saltbush LTER webs during wet productive years. Hispid pocket mice (*Chaetodipus hispidus*) were relatively common in 1992 and 1993 on yucca and

shrub-grassland (Appendix 2). I have no explanation for the apparently sporadic patterns of abundance of this or other pocket mice (*Perognathus spp.*) on the site. Pocket mice may be adundant farther east on the Pawnee National Grasslands (Mohamed 1989).

Rodent densities tend to be lower (e.g., <4 individuals/ ha of a given species) on shortgrass steppe than on other grasslands (Grant and Birney 1979). However, previous studies of rodents on shortgrass steppe (Flake 1971, Abramsky 1977, Grant et al. 1977) trapped only grassland areas, where densities and diversity of rodents are particularly low compared to areas with shrubs (Fig. 6.3). For example, in a comparison of grassland rodent communities, Grant and Birney (1979) included only four species from northern shortgrass prairie; eight species of small rodents (including northern pocket gophers, *Thomomys talpoides*) have been captured during our monitoring studies. Overall, 16 rodent species have been captured or seen on the site (Appendix 1), which is comparable to that found on other grasslands (e.g., 17 species each on desert grassland and tallgrass prairie; Packard 1971, Finck et al. 1986). Many of these species are uncommon or rare, but inclusion of different vegetation cover types in sampling efforts provided a clearer picture of both current and potential diversity of small mammals on shortgrass steppe.

Lagomorphs

The number of lagomorphs sighted on the transect ranged from 44 animals in July 1994 to 17 animals in July 1995 (mean±standard deviation = 29.8±11.9). Because ≤ 3 individuals of *Lepus townsendii* were sighted during any sampling period, I pooled observations of both *Lepus* species to estimate density, and then partitioned density according to the relative frequency of each species in the sampling period.

Sylvilagus audubonii and *L. californicus* were the most abundant species, whereas *L. townsendii* was always uncommon (Fig. 6.4). It is difficult to discern seasonal patterns with these limited data, but densities were generally lower in winter. Compared to 1994, densities of all species were extremely low in July 1995 (Fig. 6.4), but it is not clear at this point which, if either, year was unusual. Lim (1987) reported that hare densities were inversely

related to moisture during the growing season; on the CPER, the summer of 1994 was extremely hot and dry, whereas spring and early summer 1995 was unusually wet.

My results are qualitatively similar to those reported during the Grassland Biome sampling [Fig. 6.4; data from Flinders and Hansen (1973) and Flinders and Hansen (1975)], in which densities of *L. californicus* were approximately three times higher than those of *L. townsendii* (Donoho 1971). Flinders and Hansen (1973, 1975) noted the habitat separation between these species on shortgrass steppe, with *L. townsendii* more abundant on grassland and *L. californicus* in areas with saltbush and other shrubs. *L. townsendii* may be more common to the east on the Pawnee National Grasslands (Gross 1969), but Armstrong (1972) suggested that agricultural practices and grazing have improved habitat for *L. californicus*, which may be competitively superior to *L. townsendii* (Flinders and Hansen 1972).

The lagomorph census route was selected to sample representative vegetation on shortgrass steppe, and includes upland prairie, saltbush and yucca-dominated areas, and agricultural plantings (e.g., *Medicago sativa*, seeded grasses such as *Agropyron cristatum*). Accessibility to vehicles during all seasons was also considered. It has been widely-noted that vegetation along roadsides may be unnatural and that censuses conducted along roads violate the assumption that transects are located at random with respect to objects being sampled. On shortgrass steppe, roadside vegetation typically consists of weedy and annual species that provide more cover and potentially, more food plants for herbivorous species such as lagomorphs. However, <9 km (28%) of the route occurs along gravel roads (Weld County Roads 37, 114, and 122); most of the route consists of two-track trails along pasture fencelines, where vegetation resembles that of the surrounding area.

Conclusions and future directions

My results represent slightly more than one year of what is intended to be a long-term study of the population and community dynamics of small mammals on shortgrass steppe. As such, the value of these results can only be appreciated in the context of the results of future monitoring work on the site. Several general conclusions, however, emerge from these

studies to date. First, densities of nocturnal rodents are relatively low compared to more productive grasslands (Grant and Birney 1979) and the community is dominated by murid omnivores and a heteromyid granivore. *S. tridecemlineatus*, an omnivorous sciurid, accounts for a significant component of the small mammal biomass in the absence of prairie dogs (*Cynomys ludovicianus*), which were present on the CPER until recently, when the few small colonies present vanished. Furthermore, densities of all rodent species are much lower on upland grasslands than in shrub-dominated lowlands. Because grasslands are the dominant vegetation type on shortgrass steppe, previous studies of small mammals have focused on these areas, which perhaps has contributed to the perception that small mammals are minor or unimportant components of the shortgrass-steppe biota. Heterogeneity in both vegetation structure and in the abundance of seeds, however, may allow the establishment of other species such as voles and pocket mice, so that species richness, if not abundance, of small mammals on shortgrass steppe are comparable those reported for more productive grasslands.

Second, using the Grassland Biome studies conducted in the early 1970's as a reference, lagomorph populations on the study area appear to be relatively stable, although densities may fluctuate seasonally. *Lepus californicus* remains the dominant lagomorph species on the CPER, in terms of both biomass and numbers. It is not clear whether the abundance of *L. townsendii* reflects expansion and exclusion by *L. californicus* in response to rangeland practices or inadequate sampling of *L. townsendii* habitat. Comparison of rabbit locations with vegetation and habitat features (e.g., stock tanks, windbreaks) along the survey route will eventually provide a relative broad measure of habitat use. The current monitoring studies also will document the seasonal dynamics of these species more completely than previous studies. These data will be useful in studies of predator populations on shortgrass steppe because of the importance of lagomorphs in the diet of coyotes (*Canis latrans*) and many raptors (e.g. Olendorff 1973, Zimmerman et al. in press). Regular seasonal collections of scats of coyotes and swift foxes (*Vulpes velox*) along the lagomorph survey route also began in 1994 (P. Stapp and M. Lindquist, unpublished data) and may provide a measure of

temporal variation in the relative abundance of these species in the absence of detailed population studies.

Lastly, the current monitoring efforts are not effective for tracking populations of two important small mammals (*Spermophilus tridecemlineatus*, *Thomomys talpoides*) on the study area. Preliminary efforts at diurnal trapping of ground squirrels on the trapping webs were successful (L. Higgins and P. Stapp, unpubl. data), and similar procedures can be added to current monitoring studies with relatively little additional effort. In other regions, pocket-gopher densities have been estimated by counting mounds (Reid et al. 1966), which in themselves may be used to estimate relative abundance (Huntly and Inouye 1988). Determining population density from mound counts, however, ultimately requires concurrent trapping of individuals. Finally, there currently are no procedures in place for monitoring populations of amphibians and reptiles on shortgrass steppe. Such efforts should be implemented within the monitoring framework of the LTER project because the specific habitat requirements of many of these species make them particularly sensitive to changes in land-use practices, and because of recent concern over potential large-scale declines of certain herptofauna (e.g., Blaustein and Wake 1990).

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Table 6.1. Means for vegetation variables on small-mammal trapping webs (n=3 webs for each vegetation type), with standard errors provided in parentheses. Asterisks denote variables that were significantly different between vegetation types (nested ANOVA, $P \leq 0.05$).

Vegetation variable	Grassland webs	Saltbush webs
Mean vegetation height[a] (cm)	18.94 (1.57)	24.44 (6.42)
Percent saltbush cover (%)	0 (0) *	4.45 (0.84)
Mean saltbush height (cm)	0 (0) *	52.23 (2.39)
Number of burrows / ha	89.29 (10.32) *	220.25 (46.50)
Canopy cover[b] (%)		
Bare ground	13.72 (1.98) *	6.17 (1.21)
Short-grass	53.89 (10.21)	39.78 (3.48)
Mid-grass	6.28 (1.16)	13.72 (8.19)
Cactus	5.89 (1.39)	2.94 (1.29)
Forb	12.17 (1.44)	17.22 (6.50)
Small shrub (< 0.3 m)	7.72 (4.86)	13.28 (3.80)
Large shrub (≥ 0.3 m)	0 (0) *	6.00 (1.17)

[a] mean height of vegetation, excluding saltbush.

[b] percent canopy cover 0.2-m^2 point frames.

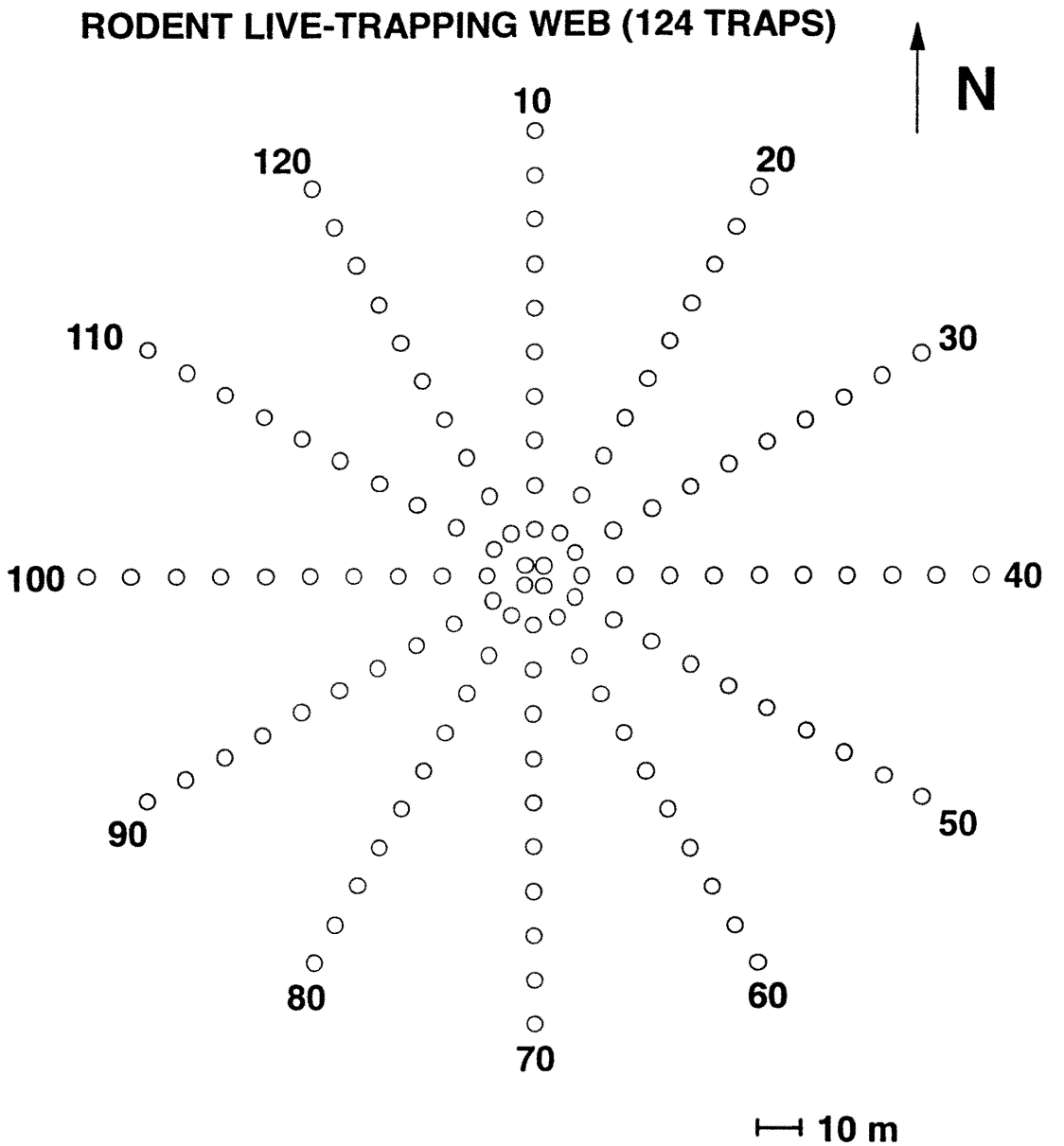

Fig. 6.1. Schematic of 3.14-ha trapping web used to sample rodent populations on the Central Plains Experimental Range. Ten large Sherman traps were placed at 10-m intervals on each of the 12 transects and four traps were placed at the center of the web.

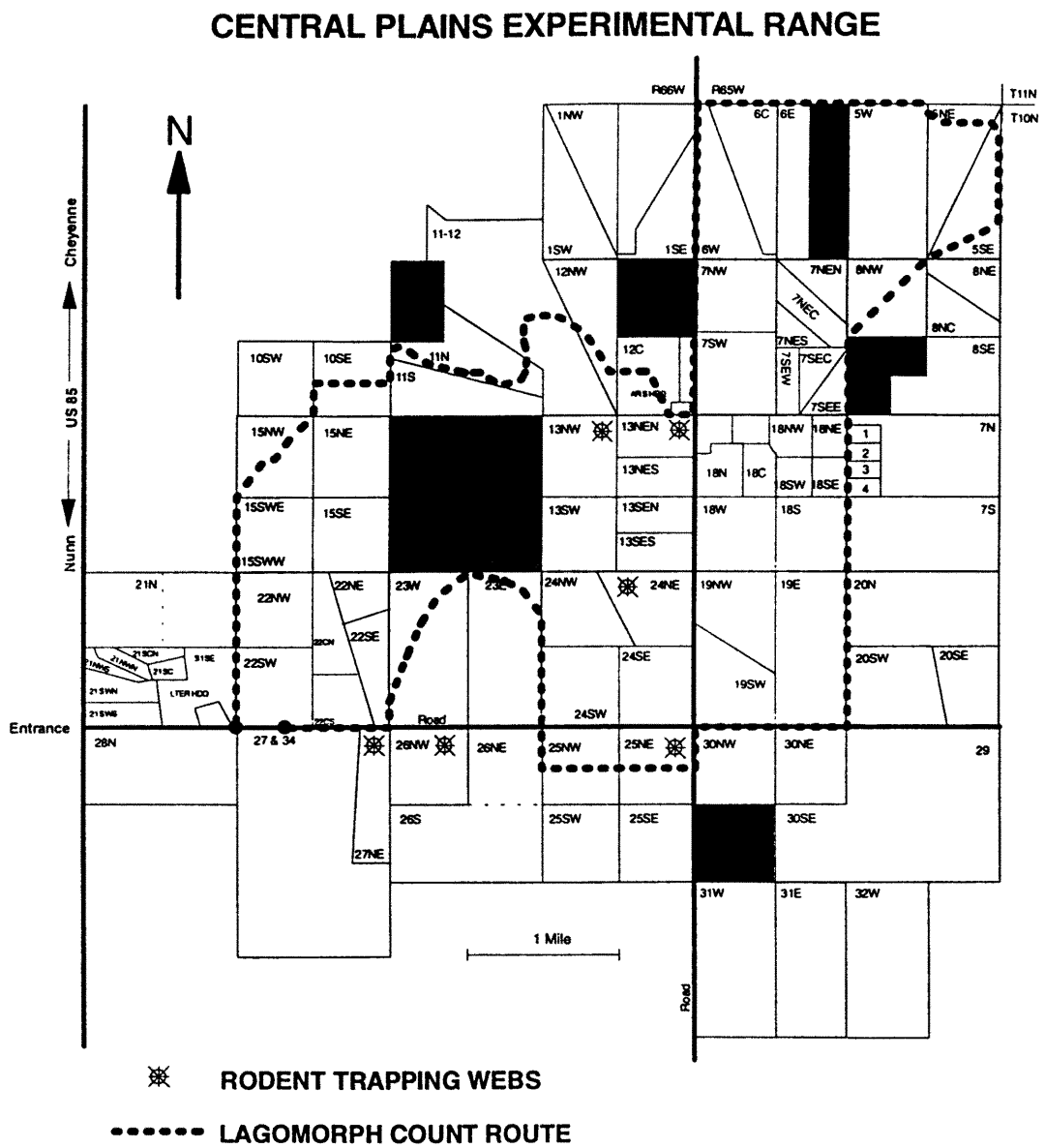

Fig. 6.2. Map showing the locations of trapping webs and the lagomorph census route on the Central Plains Experimental Range, north-central Colorado. Grassland webs are located in pastures 27NE, 26NW, and 25NE. Saltbush webs are located in pastures 13NW, 13NEN, and 24NE.

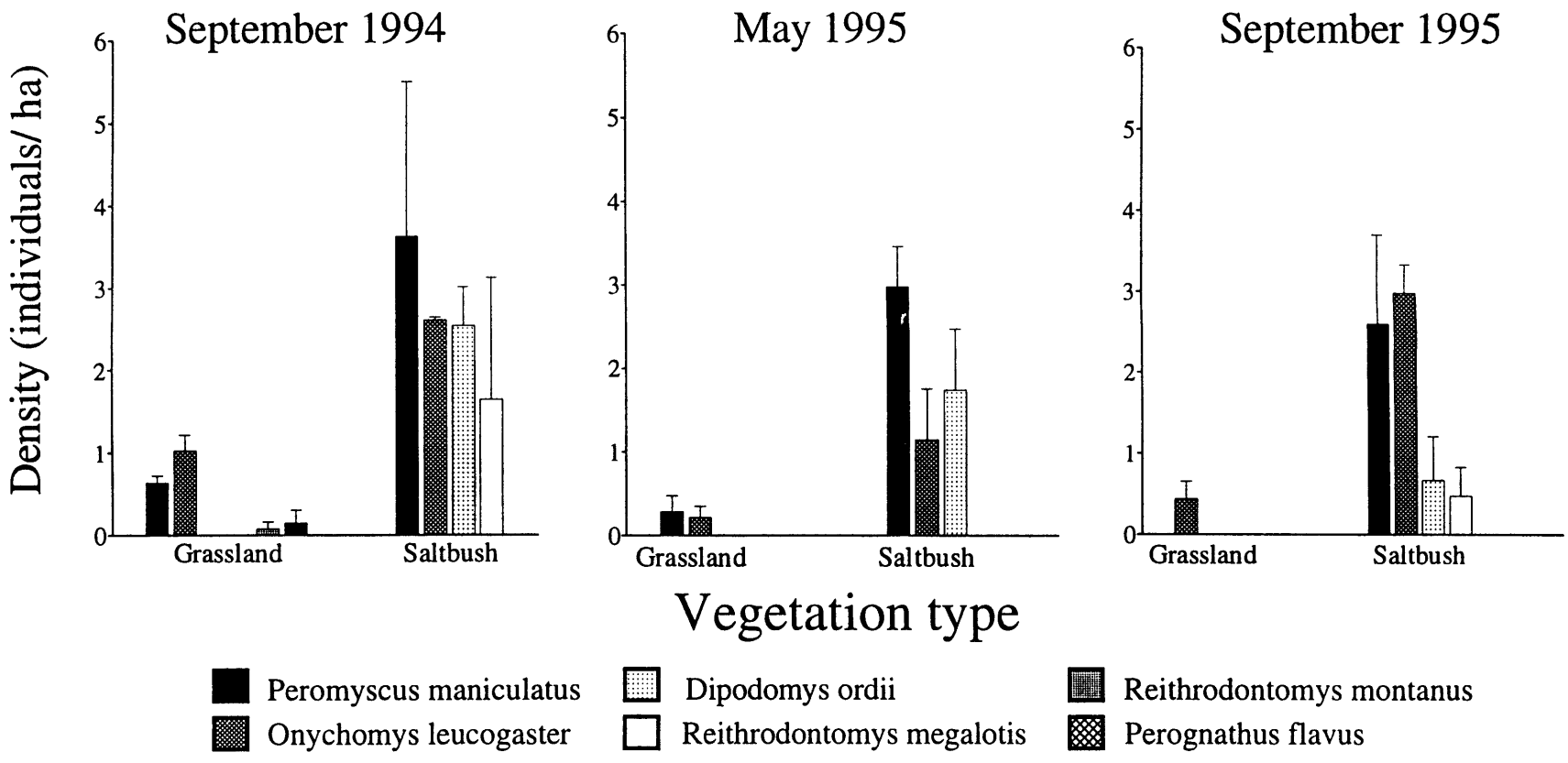

Fig. 6.3. Density (number of individuals/ha) of small nocturnal rodents on grassland and saltbush trapping webs on the Shortgrass Steppe LTER site in a) September 1994, b) May 1995, and c) September 1995.

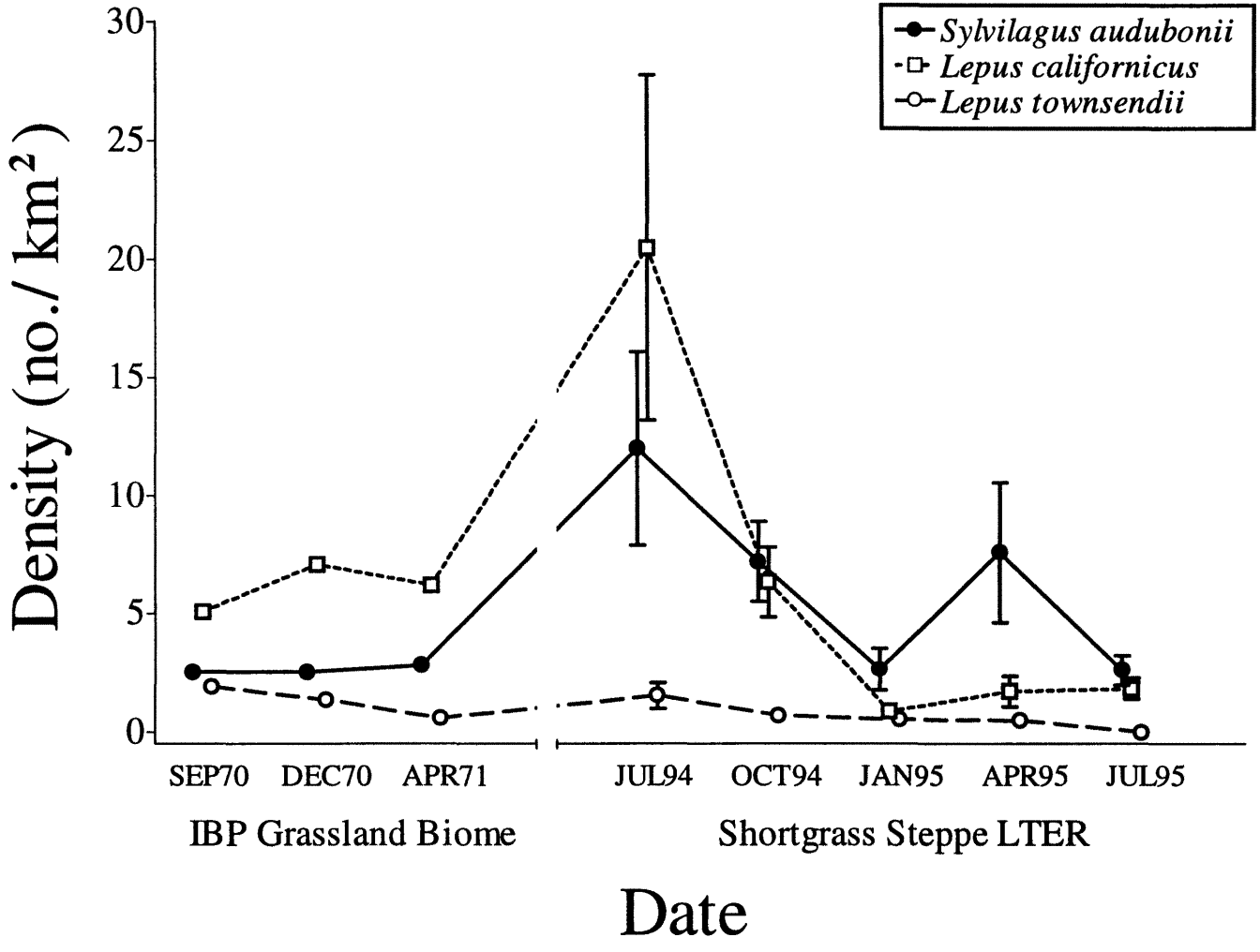

Fig. 6.4. Density of lagomorphs on the Central Plains Experimental Range during censuses conducted during the US/IBP Grassland Biome project (1970-1971) and the Shortgrass Steppe LTER project (1994-1995). IBP data derived information in Flinders and Hansen (1973) and Flinders and Hansen (1975; moderately-grazed pastures).

Appendix 1. Mammals of the Shortgrass Steppe Long-Term Ecological Research site, including the Pawnee National Grasslands, Weld County, Colorado. Asterisks denote species seen or captured on and adjacent to the Central Plains Experimental Range between 1992-1996 (P. Stapp, unpublished data). Crosses denote species captured during live-trapping studies. Taxonomic designations follow Fitzgerald et al. (1994).

O. Insectivora	
F. Soricidae	
Least shrew	Cryptotis parva parva
O. Chiroptera	
F. Vespertilionidae	
Western small-footed myotis	Myotis ciliolabrum ciliolabrum
Big brown bat	Eptesicus fuscus pallidus
Silver-haired bat	Lasionycteris noctivagans
Hoary bat	Lasiurus cinereus cinereus
O. Lagomorpha	
F. Leporidae	
Desert cottontail	Sylvilagus audubonii baileyi*
Black-tailed jackrabbit	Lepus californicus melanotis*
White-tailed jackrabbit	Lepus townsendii campanius*
O. Rodentia	
F. Sciuridae	
Black-tailed prairie dog	Cynomys ludovicianus ludovicianus*
Thirteen-lined ground squirrel	Spermophilus tridecemlineatus pallidus†*
Spotted ground squirrel	Spermophilus spilosoma obsoletus
Fox squirrel	Sciurus niger rufiventer*
F. Geomyidae	
Northern pocket gopher	Thomomys talpoides attenuatus†*
Plains pocket gopher	Geomys bursarius lutescens
F. Heteromyidae	
Olive-backed pocket mouse	Perognathus fasciatus infraluteus †*
Plains pocket mouse	Perognathus flavescens flavescens
Silky pocket mouse	Perognathus flavus bunkeri†*
Hispid pocket mouse	Chaetodipus hispidus paradoxus†*
Ord's kangaroo rat	Dipodomys ordii luteolus†*
F. Castoridae	
Beaver	Castor canadensis concisor*
F. Muridae	
Plains harvest mouse	Reithrodontomys montanus albescens†*
Western harvest mouse	Reithrodontomys megalotis dychei†*
Deer mouse	Peromyscus maniculatus nebrascensis†*
Northern grasshopper mouse	Onychomys leucogaster arcticeps†*

Appendix 1. continued

Bushy-tailed woodrat	Neotoma cinerea rupicola
Prairie vole	Microtus ochrogaster haydeniit*
Meadow vole	Microtus pennsylvanicus uligocola
Muskrat	Ondatra zibethicus cinnamominus
House mouse	Mus musculust*
F. Erethizontidae	
Porcupine	Erethizon dorsatum bruneri*
O. Carnivora	
F. Canidae	
Coyote	Canis latrans latrans*
Swift fox	Vulpes velox velox*
Red fox	Vulpes vulpes macroura*
F. Procyonidae	
Raccoon	Procyon lotor hirtus
F. Mustelidae	
Long-tailed weasel	Mustela frenata longicaudat*
Badger	Taxidea taxus taxus*
Striped skunk	Mephitis mephitis hudsonica*
F. Felidae	
Bobcat	Lynx rufus rufus*
O. Artiodactyla	
F. Cervidae	
Mule deer	Odocoileus hemionus hemionus*
White-tailed deer	Odocoileus virginiana dacotensis*
F. Antilocapridae	
Pronghorn	Antilocapra americana americana*

Appendix 2. Density and sex ratio (M:F:unknown) of small rodents on three grids during 5 consecutive nights of trapping between July 1992 and December 1993. In July 1992, grids were 2.72 ha and consisted of a 12 by 12 array with 15-m spacing (144 traps). During all other periods, grids were 1.82 ha, with 100 traps in a 10 by 10 array. Densities were calculated by dividing the number of individuals captured by effective trapping area. Effective trapping area was estimated as the area bounded by the traps plus a 20-m boundary strip, which was based on estimates of movement distances of the three most common species (*Peromyscus maniculatus*, *Onychomys leucogaster*, *Dipodomys ordii*). Species abbreviations: PEMA, deer mouse; ONLE, northern grasshopper mouse; REME, western harvest mouse; REMO, plains harvest mouse; MIOC, prairie vole; DIOR, Ord's kangaroo rat; CHHI, Chaetodipus hispidus; SPTR, thirteen-lined ground squirrel; MUMU, house mouse.

	Saltbush floodplain (11% saltbush)	Shrub grassland (4% saltbush)	Yucca prairie (1% yucca)
JULY 1992			
PEMA	5.71 (15:9)	1.19 (4:1)	1.90 (5:3)
ONLE	0	2.14 (3:6)	2.86 (5:7)
REME	2.14 (5:4)	0	0
REMO	0	0.24 (0:1)	0
MIOC	0.48 (1:1)	0	0
DIOR	0	0.48 (1:1)	1.90 (4:4)
CHHI	0	0.71 (1:2)	1.67 (3:4)
SPTR[a]	0.95	2.14	1.67
DECEMBER 1992			
PEMA	3.92 (7:5)	1.31 (2:2)	2.61 (7:1)
ONLE	0	0.98 (1:2)	0
REME	2.61 (3:5)	0	0
REMO	2.61 (1:7)	0.33 (1:0)	0.65 (2:0)
MIOC	0.665 (2:0)	0.33 (1:0)	0.33 (1:0)
DIOR	0	1.31 (0:4)	0

Appendix 2. continued	Saltbush floodplain (11% saltbush)	Shrub grassland (4% saltbush)	Yucca prairie (1% yucca)
MAY 1993			
PEMA	4.25 (10:3)	3.27 (5:5)	2.29 (4:2:1)
ONLE	0	2.94 (4:5)	2.61 (4:4)
REME	1.63 (3:2)	0	0
REMO	0	0.33 (1:0)	0.33 (1:0)
DIOR	0	3.59 (6:5)	2.94 (4:4:1)
CHHI	0	0.33 (1:0)	0
MUMU	0.33 (1:0)	0	0
SPTR[a]	0.33	0.33	0
JULY 1993			
PEMA	4.25 (8:5)	2.61 (7:1)	2.29 (4:3)
ONLE	0.33 (0:1)	1.96 (2:4)	2.61 (5:3)
REME	4.25 (7:6)	0	0
DIOR	0.33 (1:0)	2.29 (3:4)	2.94 (5:4)
CHHI	0	0.98 (0:3)	0.33 (0:1)
SPTR[a]	0.33	3.92	0
DECEMBER 1993			
PEMA	4.90 (11:4)	0.33 (1:0)	0.33 (1:0)
ONLE	0.65 (1:1)	0.98 (1:2)	0
REME	2.29 (3:4)	0	0
REMO	1.63 (3:2)	0	0.33 (1:0)
DIOR	0	0.65 (2:0)	0

[a] Captures of *Spermophilus tridecemlineatus* were incidental because traps were set and checked when diurnal squirrels were not active.

Appendix 3. Mean maximum distance (m) between captures of deer mice (*Peromyscus maniculatus*), northern grasshopper mice (*Onychomys leucogaster*), Ord's kangaroo rats (*Dipodomys ordii*), and western harvest mice (*Reithrodontomys megalotis*) during 5-night trapping sessions on three trapping areas between July 1992 and December 1993 (see Appendix 2). Means were calculated for each area and season separately; values are the means and standard errors (in parentheses) for n trapping sessions, combining across areas and seasons. Only sessions in which >1 individual was captured at >1 trap station were included in means.

Species	n	Mean maximum distance (m)
Peromyscus maniculatus	14	36.30 (2.64)
Onychomys leucogaster	6	53.70 (8.71)
Dipodomys ordii	5	29.50 (3.79)
Reithrodontomys megalotis	5	21.54 (4.90)