ABSTRACT

Effects of Habitat Affinities and Resource Needs on Edge Responses by Small Mammals

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Edge effects are the responses of organisms to ecological boundaries. I studied edge responses by small mammals in two prairie communities to test two models: 1) edge responses reflect and map to simple habitat associations, and 2) edge responses reflect differences in resource availability on either side of an edge. I also investigated how edge contrast, the degree of difference between habitats at an edge, could modify edge responses. Pilot sampling in 2009 and 2010 at a Blackland prairie preserve revealed that hispid cotton rats (*Sigmodon hispidus* Say and Ord 1825) responded negatively to edges of wooded patches and weakly positively to edges between tallgrass and dicot forbs. Deer mice (*Peromyscus maniculatus* (Wagner 1845)) and fulvous harvest mice (*Reithrodontomys fulvescens* Allen 1894) did not respond to habitat edges, although this may have been an artifact of low capture rate (especially in 2010). Sampling in 2011 at the Lyndon B. Johnson National Grasslands (LBJNG), a mixed grass preserve, found that *S. hispidus* responded negatively to edges where dense grass abutted dicot forbs or wooded patches. These edge effects reflected the strong association of *S. hispidus* with grassland habitat. Sampling of leptin, a hormone secreted by adipose tissue and

associated with energy intake in many species, revealed that serum leptin concentration (SLC) was limited by body mass and not associated with any other organismal characteristic. Among male *S. hispidus* SLC was limited by food availability and among females the lower limit of SLC decreased with increasing grass cover. This suggests that if *S. hispidus* edge responses are caused by resource mapping, the critical resource is not nutrition. Other species at LBJNG, *P. maniculatus* and hispid pocket mice (*Chaetodipus hispidus* (Baird 1858)) were associated with habitats with intermediate ground cover and did not show clear edge responses. I concluded that 1) when prairie dwelling small mammals respond to edges, they are more likely to show matrix effects (response to nonhabitat) than ecotonal effects (emergent properties at boundaries); and 2) small mammal abundances and edge responses are driven by resources other than nutrition.

Effects of Habitat Affinities and Resource Needs on Edge Responses by Small Mammals

by

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A Dissertation

Approved by the Department of Biology

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DEDICATION

To my family, for always giving me enough courage to leave the nest,
and enough love to always want to come back

CHAPTER ONE

Introduction

Edges in Ecology

Edge effects are the responses of organisms to ecological boundaries. The concept of ecological edges as boundaries between habitat types was first elaborated by Clements (1905) and was introduced to animal ecology by Leopold (1933). Subsequent generations refined the concept to define habitats by plant communities and to accommodate individualistic edge responses (Di Castri et al. 1988; Lidicker and Peterson 1999). Edges present gradients in biotic factors, such as vegetative composition, predator abundance, and food abundance, as well as abiotic factors such as light, temperature, soil moisture, and wind exposure (Chen et al. 1999; Meyer et al. 2001; Weathers et al. 2001; Cadenasso et al. 2003). From a mobile organism's point of view, an ecological boundary represents a spatial gradient or discontinuity in the availability of resources. Animals responding to habitat edges are often responding to the changes in the composition or structure of vegetation at the edge (Kingston and Morris 2000; Ries et al. 2004).

Terminology to describe edges has evolved over time. The original "zone of tension" or ecotone described by Clements (1905) has been elaborated to include several closely related concepts. The original meaning of ecotone was a meeting of two plant communities, including the *boundary* or demarcation line between the communities and some edge zone between the communities (Wiens et al. 1985). This edge habitat may or may not have emergent characteristics setting it apart from the plant communities on either side (Strayer et al. 2003). More recently, because of growing appreciation for the

importance of spatial scale in ecology, ecotone has come to mean large-scale gradients in habitat while *edge* and *boundary* describe habitat transitions over much shorter distances (Cadenasso et al. 2003). For example, the edge of a patch of forest on a prairie landscape, where the forest to grassland transition happens on a scale of meters, could be called a boundary or an edge (Cadenasso et al. 2003). A gradient from freshwater streams to the ocean over a scale of kilometers would be considered an ecotone (Winemiller and Leslie 1992). In this dissertation, the edges studied are boundaries at spatial scales relevant to small mammal foraging activity—meters to tens of meters (Morris 1992; Zollner and Lima 1997)—so edge and boundary are used interchangeably.

The underlying mechanisms of edge responses are not well understood but several models have been proposed. The framework of Lidicker and Peterson (1999) is particularly useful because its corollaries address the specificity of edge responses to single species or age or sex classes, the effects of edges on organism performance, the possibility of different edge effects from different edge types, and the difficulty of recognizing some edges. They suggested a two-part classification of "matrix" and "ecotonal" effects (Figure 1).

Edge responses that can be predicted solely by a species' response to the abutting habitats in isolation are matrix effects, while edge responses not predicted by simple habitat associations are ecotonal effects. *Matrix effects* lack emergent properties and are caused by the mapping of some response variable (abundance, reproductive rates, animal performance, etc.) onto the more suitable and less suitable habitats at the edge. Strayer et al. (2003) called these "*noninteractive*" boundary effects, and describe conditions near the boundary as a simple average of the conditions in patches on either side. *Ecotonal*

effects are characterized by emergent properties in the response variable that differ from patterns in the adjacent habitats. These emergent properties make them "*interactive*" boundaries in the framework of Strayer et al. (2003). Lidicker (1999, p 337) notes that while it may be difficult to distinguish which type of edge effect is being observed, the matrix effect should be the null hypothesis because "it should be possible to make a clear prediction of the resulting edge response knowing the values of the variables in each habitat-type separately, and assessing the degree of blending on the edge."

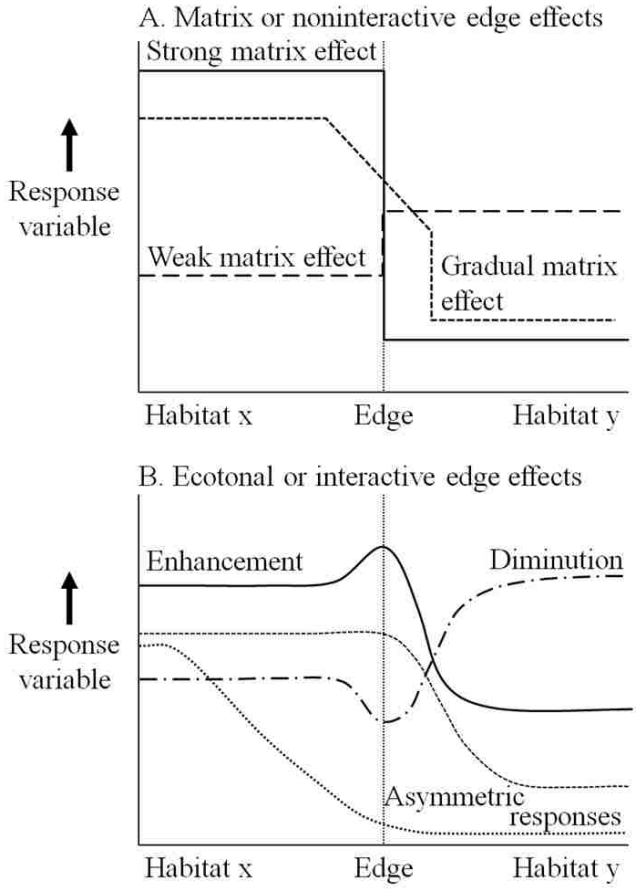

Figure 1. Matrix effects (A) are changes in some response variable caused by a sharp difference between habitat (x) and nonhabitat (y) at an edge that directly reflect differences in habitat quality. Ecotonal effects (B) are changes in response variables that are not directly attributable to differences between habitats x and y. Figure redrawn from Lidicker (1999), Strayer et al. (2003)

More recently the resource-distribution model (Ries and Sisk 2004) uses an expanded definition of resource to predict the direction of edge responses. In this model, a *resource* is any biotic or abiotic condition that an organism requires for survival or reproduction. The resource in question could be biotic (e.g., the absence of predators or surfeit of food) or abiotic (e.g., tolerable temperatures or adequate water). In this model, the nature of edge effects depends on whether resources on either side of a boundary are supplementary (i.e., each habitat contains the same types of resources, but in differing abundance) or complementary (i.e., each habitat contains qualitatively different resources required by the organism; Dunning et al. 1992). In their model, resource complementarity causes positive edge effects on both sides of the boundary. When resources are supplementary, edge responses will be neutral (or nonexistent) when habitats are similar and transitional (i.e., negative in more suitable habitats and positive in the less suitable habitat) when habitats are dissimilar (Figure 2).

An important implication of this model is that all species are predicted to show positive, neutral, and negative edge responses, depending on the ecological context of the edge. This model has performed well in meta-analyses (Ries et al. 2004) and experimental studies of riparian butterflies (Ries and Sisk 2008) and carabid beetles (Noreika and Kotze 2012).

The degree of difference or habitat contrast (Stamps et al. 1987; Strayer et al. 2003) can mediate edge responses (Figure 3). Similarity between habitat patches and surrounding matrix affects dynamics both within individual patches and between patches (Prevedello and Vieira 2010). In any model the differences between the habitats meeting at an edge are what cause any edge effect.

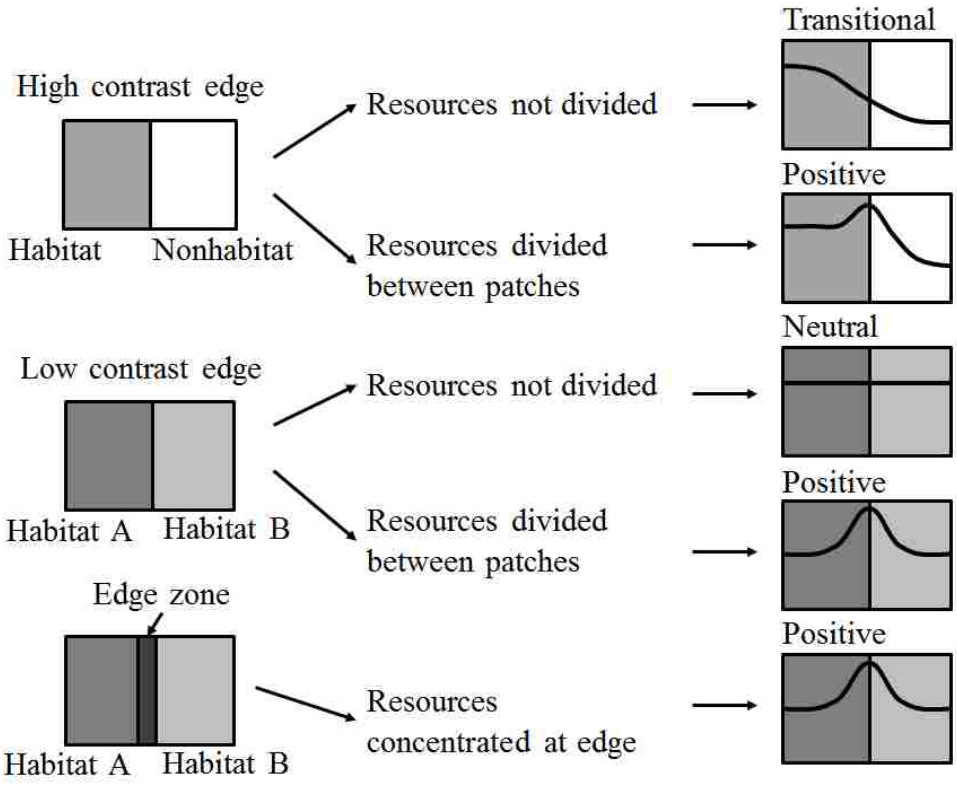

Figure 2. The resource distribution model predicts matrix effects similar to Lidicker and Peterson (1999) when habitats differed greatly at an edge and resources were complementary and a positive ecotonal effect when resources were complementary. When the habitats at an edge contrasted less, edge responses are expected to be neutral when resources are supplementary and positive is resources are complementary or concentrated at an edge. Figure modified and redrawn from Ries et al. (2004)

Edge contrast is thought to affect the magnitude of an edge effect much more than its direction (Ries et al. 2008). Correlation of edge effect magnitude with habitat contrast has been observed in bobolinks (*Dolichonyx oryzivorus* (Linnaeus 1758); Fletcher and Koford 2003) and grassland butterflies (Ries and Debinski 2001). Spencer et al. (1983) and Chapin and Harrison (1998) found that martens (*Martes americana* (Turton 1806)) routinely occupied edges where the habitats on either side differed less from each other than did the two sharply contrasted habitats in the landscapes studied by Hargis et al. (1999). This difference in the use of edges may be because low-contrast edges are used

more by martens, or because the reduced marten abundance at edges is a result of the loss of interior habitat and edge prevalence is merely a covariate.

Figure 3. Examples of a high contrast edge (left) and low contrast edge (right) at the LBJ National Grasslands in 2011. Habitats on either side of the high contrast edge have very different ground cover while habitats on either side of the low contrast edge have similar ground cover

Patch contrast plays an important role in the movements of small mammals near edges. Desrochers et al. (2003) found that Siberian flying squirrel (*Pteromys volans* (Linneaus 1758)) densities were higher in low-contrast edge habitat than in high-contrast habitats. Flying squirrels tended to avoid edges between spruce forest "nesting habitat" and open habitat which provided nothing from which to leap. *Pteromys volans* was more abundant in edges between spruce forest and "movement habitat," or forest types other than mature spruce stands. Lopez-Barrera et al. (2007) found that high-contrast edges presented a highly impermeable barrier to movement out of a forest for small mammals. Both of these studies found that high habitat contrast appears to block movement across the edge and instead direct movement parallel to the edge. The findings of these two studies indicate that high-contrast edges seem to have absorptive or reflective effects on

small mammal movements, while low-contrast edges are either neutral, transmissive, or amplificatory (Strayer et al. 2003).

Quantification of habitat contrast and habitat suitability might enable better predicton of edge effects. Quantitative measures of contrast can be as simple as an absolute difference in one variable or can be multivariate. For example, Watling and Orrock (2010) measured univariate abiotic edge contrast as the absolute difference in light penetration of forest canopy.

Measuring Body Condition

The most direct way to measure the suitability of a habitat for an organism is to measure some physiological index of body condition. Body condition is a general term for the overall health of an animal, which is usually indicative of nutritional status (Stevenson and Woods 2006). If edge habitats are poor for foraging (Wolf and Batzli 2004), then animals captured in these habitats should be in significantly poorer body condition than animals captured in interior habitat.

Many different characteristics have been used as indices of body condition, including residuals of body mass to length regressions (Green 2001; Schulte-Hostedde et al. 2001), weight to mass ratios (McMurry et al. 1995), morphometric scaling relationships (Berger and Peacock 1988), and multivariate methods (Blackwell 2002). Current morphological measures of small mammal foraging activity are imprecise at best and fatal at worst (Green 2001; Hayes and Shonkwiler 2001). Seed removal can measure the intensity of foraging but not the benefit of foraging to individual organisms. Body mass and external measurements are highly variable and confounded with age, gender,

and other proximate factors (Krebs and Singleton 1993; Hayes and Shonkwiler 2001; Wauters et al. 2007). The morphology of an organism is less responsive to the environment than are physiology and behavior (Ricklefs and Miles 1994; Landry and LaPointe 2001). Chemical body composition measurements require the destruction of the animal, making it unattractive as a technique in protected or small populations.

Fat mass percentage (FMP) is an intuitively appealing index because it is directly correlated with food intake (and presumably habitat quality) in many mammals (Fleharty et al. 1973; Kołodziej-Banach 1976; Chilliard 1993). While laboratory studies have shown a strong such correlation, this relationship in wild rodents is less clear. Studies of brown lemmings (*Lemmus sibiricus* (Kerr 1792)) and white-footed deer mice (*Peromyscus leucopus* (Rafinesque 1818)) have revealed that FMP can be a misleading body condition index in wild organisms during late spring and early summer, when many small mammals invest excess energy in reproductive effort rather than stores of body fat (Millar 1981; Batzli and Esseks 1992) although Lochmiller et al. (1983) found the opposite to be true in pine voles (*Microtus pinetorum* (LeConte 1830)) when the effects of season and reproductive condition were accounted for. The authors of those studies recommend alternative approaches to quantifying small mammal body condition.

Measuring body fat in small mammals directly can be difficult. The traditional method requires sacrificing, homogenizing, and drying the animal, then extracting its lipids with a solvent in a Soxhlet or similar apparatus (Reynolds and Kunz 2001). While this process yields very precise results, the destruction of large numbers of animals is ethically dubious and ultimately unnecessary if suitable alternative measures can be found. Some recently developed techniques include total-body electrical conductivity

(Scott et al. 2001), bioelectric impedance analysis (Van Lichtenbelt 2001), ultrasound imagery (Starck et al. 2001), and dual-energy X-ray absorbiometry (Nagy 2001). All of these techniques can estimate total percentage body fat with varying degrees of effectiveness, but the drawbacks of high cost, long processing time, and lack of portability make them prohibitive to use in a study of small mammal ecology.

Leptin is a hormone produced by adipose tissue whose concentration in blood plasma is positively and strongly correlated with body fat percentage (Hamilton et al. 1995; Maffei et al. 1995; Klein et al. 1996) and food intake regardless of FMP (Ahima et al. 1996; Ahren et al. 1997; Dubuc et al. 1998; Reidy and Weber 2000); thus, by 2 separate pathways leptin may be suitable as a direct indicator of body condition and an indirect indicator of forage quality within a habitat. Nieminen (2000) found that leptin did not correlate directly with body mass index (BMI) in common shrew (*Sorex araneus* Linnaeus 1758), mink (*Neovison vison* (Schreber 1777)), raccoon dog (*Nyctereutes procyonoides* (Gray 1834)) and blue fox (*Vulpes lagopus* (Linnaeus 1758)) but rather with satiety. In mammals, leptin regulates appetite and lipid reserves (Reidy and Weber 2000), puberty and reproduction (Cunningham et al. 1999; Margetic et al. 2002), and body temperature (Henry et al. 2011). Circulating levels of leptin in the blood are strongly tied to a mammal's energy balance, and several studies have found that leptin helps mediate energy metabolism independent of food intake (Elmquist 2001; Rayner and Trayhurn 2001; Margetic et al. 2002). Because of its production by adipose tissue and function as a satiety signal, it is predicted that leptin will be positively correlated with body condition and habitat quality.

Objectives

Dissertation Questions

The overall objective of the dissertation was to investigate why small mammals associate with habitats and respond to edges. Questions 1, 2, 3, and 4 apply to all species for which there are sufficient data. Questions 2, 3, 4, and 5, regarding different models of edge effects, are the primary questions of this dissertation. Questions 6, 7, 8, and 9 are supplementary and only apply to *S. hispidus*.

1. Habitat Association

Every species has unique resource and space requirements, so small mammal species should be associated particular habitat types. When a species is found, it should be associated with some habitats more than others. This association could be continuous (abundance correlated with some measure of habitat quality) or discrete (abundance differs between habitat types).

H_0: Abundance will not differ between sampling grids in different plant communities.

H_a: Abundance will differ between sampling grids in different plant communities.

2. Edge Effects as Matrix Effects

If edge effects result from the meeting of suitable habitat and unsuitable habitat (i.e., matrix), then edge responses should be negative when compared to interior habitat and positive when compared to matrix interior (habitat association hypothesis; Lidicker and Peterson 1999). Put another way, edge responses should reflect simple habitat

associations. This hypothesis is one scenario (Figure 2) in the model of Ries and Sisk (2004).

H_0: Abundance does not differ between interior habitats and edges between suitable and unsuitable habitat.

H_a: Abundance differs significantly between interior habitats and edges between suitable and unsuitable habitat.

3. Edge Effects as Ecotone Effects

If the meeting of two habitat types creates a distinct "edge habitat", then edge responses should have the same sign on both sides of an edge (i.e., abundance in edge habitat is higher than or lower than both habitat and matrix interiors). Lidicker and Peterson (1999) call this an "ecotonal effect."

H_0: Abundance in the edge habitat will be lower than abundance in interior habitat and higher than abundance in the matrix habitat.

H_a: Abundance in the edge habitat will be higher than abundance in interior habitat and higher than abundance in the matrix habitat; or, abundance in the edge habitat will be lower than abundance in interior habitat and lower than abundance in the matrix habitat.

4. Edge Effects as Resource Mapping

Edge responses are determined by the distribution of resources on either side of an edge (Ries and Sisk 2004). Small mammals should respond to edges negatively when the resources in another habitat are supplementary to those in their own habitat, and should respond positively when resources in another habitat are complementary to those in their own habitat.

H_0: Species will respond negatively or not at all to an edge where the adjacent habitat has resources complementary to those in the interior habitat; species will respond positively or not at all to edges where the adjacent habitat is unsuitable or has resources supplementary to interior habitat.

H_a: Species will respond positively to an edge where the adjacent habitat has resources complementary to those in the interior habitat; species will respond negatively to edges where the adjacent habitat is unsuitable or has resources supplementary to interior habitat.

5. Alteration of Edge Effects by Habitat Contrast

If edge effects are caused by a difference in habitat suitability or resource availability, then the magnitude of an edge effect should depend on the difference between habitats.

H_0: Magnitude of an edge response is unrelated to the magnitude of difference between the habitats that meet at an edge.

H_a: Magnitude of an edge response is significantly positively correlated with the magnitude of difference between the habitats that meet at an edge.

6. Effect of Mass on Leptin in Sigmodon hispidus

If the hormone leptin is produced by adipose tissue and tied to overall energy intake, then serum leptin concentration (SLC) should vary with animal mass.

H_0: There is no correlation between SLC and body mass.

H_a: There is a significant correlation between SLC and body mass.

7. Sexual Dimorphism in Serum Leptin Concentration

If the hormone leptin is produced by adipose tissue, then the more adipose sex should have the highest SLC.

H_0: There is no difference in SLC between males (the more adipose sex) and females (the less adipose sex).

H_a: There is a significant difference in SLC between males (the more adipose sex) and females (the less adipose sex).

8. Relationship between Leptin and Food Availability

If the hormone leptin is produced by adipose tissue and associated with overall energy intake, then SLC should vary with food availability in an organism's environment. For *S. hispidus*, the species of interest, food availability is indicated by the density of grasses and dicot forbs.

H_0: There is no correlation between food availability and SLC.

H_a: There is a significant correlation between food availability and SLC.

9. Endocrine Signal of Resource Mapping in Sigmodon hispidus

If the resource that drives edge responses by *S. hispidus* is nutrition, then SLC should vary between edge habitats and interior habitats.

H_0: There is no significant difference between SLC of animals captured in interior habitats and edge habitats.

H_a: There is a significant difference between SLC of animals captured in interior habitats and edge habitats.

Outline of the Dissertation

This project began as an investigation of the effects of habitat contrast on edge responses by small mammals, but has evolved to encompass the mechanisms behind not only edge responses but habitat association in general. The following chapters describe the findings of several interrelated modules of this dissertation. In Chapter 2, I describe sampling conducted in 2009 and 2010 at a Blackland prairie preserve, Clymer Meadow, in Hunt Co., Texas. In this sampling I tested different ways of identifying habitat boundaries on a landscape and how those edges affect small mammals. My original plan was to complete sampling in the summer of 2010, but the small mammal populations at

Clymer Meadow crashed sometime between the summers of 2009 and 2010. The resulting capture rates and sample sizes in 2010 were insufficient to complete a dissertation. Instead the 2010 dataset has been repurposed as a preliminary study of edge effects.

In 2011 I chose a new field site, the Lyndon B. Johnson National Grassland (LBJNG; Wise Co., Texas), and sampled that summer. Chapters 3, 4, and 5 are formed from 3 manuscripts arising from my 2011 dataset. Chapter 3 describes the habitat associations of the 3 most common species at LBJNG and is in revision for submission to the *Southwestern Naturalist*. Chapter 4 describes organismal and environmental drivers of the hormone leptin in *S. hispidus*, and was submitted to the *Journal of Mammalogy* on 5 April 2012. Chapter 5 builds on Chapters 3 and 4, examining edge responses by 3 species and using serum leptin concentration (SLC) to make inferences about why *S. hispidus* is associated with grassland habitats and why it responds to habitat boundaries. Chapter 5 is in preparation for submission to the *Journal of Animal Ecology*, and submission is expected by 1 July 2012. A concluding chapter, Chapter 6, synthesizes the findings of the others. Selected R code is presented in the Appendix.

CHAPTER TWO

Pilot Study of Small Mammals at Clymer Meadow

Abstract

I sampled small mammal abundance and plant cover at the Clymer Meadow Preserve in Hunt County, Texas, in the summers of 2009 and 2010. Goal of sampling in 2009 was to test experimental design; 2010 was intended to be the final year of sampling but a population decline prevented meaningful data analysis. I captured 6 species of rodent in 2009 and 7 species in 2010. Deer mice (*Peromyscus maniculatus*), fulvous harvest mice (*Reithrodontomys fulvescens*) and hispid cotton rats (*Sigmodon hispidus*) were the most common species in both years. Only *S. hispidus* showed significant edge responses, avoiding wooded edges in 2009. I found no evidence of edge responses in 2010, but this may have been caused by low capture rates. I tested several methods of quantifying edge contrast and found that while some of these metrics could accurately describe edges, they were very poor predictors of rodent abundance. After the 2010 sampling season I moved to a larger field site with higher rodent abundance.

Introduction

Pilot sampling was conducted at the Clymer Meadow Preserve in 2009 and 2010. Clymer Meadow is a 432 ha preserve owned by the Nature Conservancy of Texas near Celeste, Hunt County, Texas (Figure 4). Clymer Meadow is one of the largest remaining fragments of Blackland prairie and is dominated by the indiangrass (*Sorghastrum nutans* (L.) Nash)-little bluestem (*Schizachyrium scoparium* (Michx.) Nash) series of grassland

(Diamond and Smeins 1993). The preserve is managed by The Nature Conservancy for native hay and wildlife by periodic haying, burning, and grazing cattle (*Bos taurus* Linnaeus 1758) and bison (*Bison bison* (Linnaeus 1758)). Previous small mammal surveys (Wilkins 1990, 1991, 1995; Green and Wilkins 2010) at or near Clymer Meadow had found least shrew (*Cryptotis parva* (Say 1823)), house mouse (*Mus musculus* (Linnaeus 1758)), northern pygmy mouse (*Baiomys taylori* (Thomas 1887)), eastern woodrat (*Neotoma floridana* (Ord 1818)), white-footed mouse (*Peromyscus leucopus*), deer mouse (*P. maniculatus* (Wagner 1845)), fulvous harvest mouse (*Reithrodontomys fulvescens* (Allen 1894)), eastern harvest mouse (*R. humulis* (Audubon and Bachman 1841)), hispid cotton rat (*Sigmodon hispidus*), and marsh rice rat (*Oryzomys palustris* (Harlan 1837)).

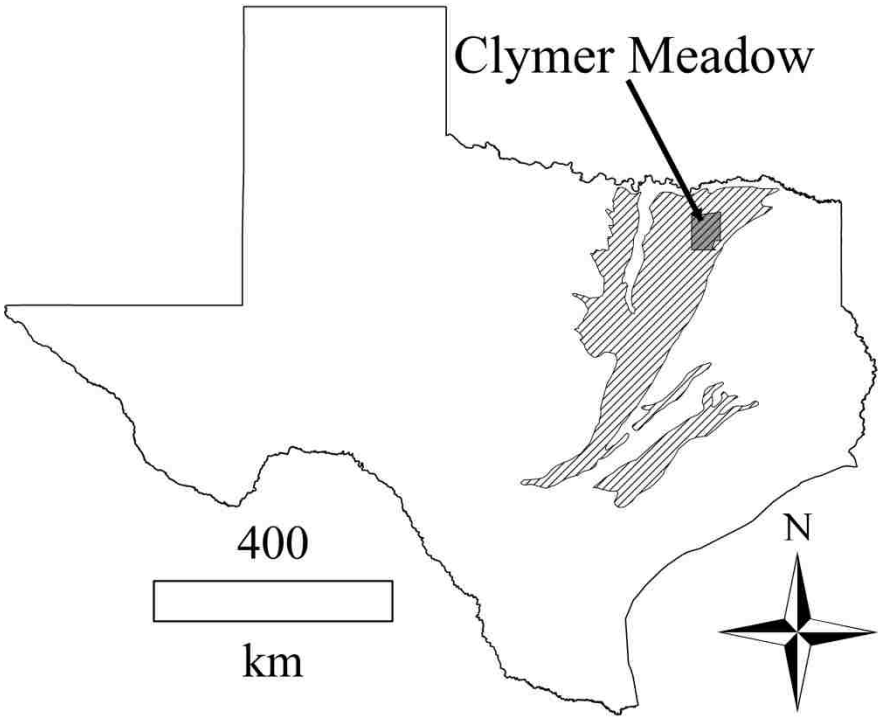

Figure 4: Location of Clymer Meadow in northwestern Hunt County, Texas (shaded grey) and its position in the Blackland Prairie ecoregion of Texas (cross hatched area)

The goal of pilot sampling was to test for edge effects in a tallgrass prairie small mammal community and to evaluate several methods for characterizing habitat edges. I hypothesized that grassland associated species (*B. taylori*, *R. fulvescens*, and *S. hispidus*) would respond negatively to edges between grassland and nongrass habitat and that the generalist species *P. maniculatus* would not respond to habitat edges. I also expected that edge effects would be stronger when the contrast between habitats at an edge was greater.

Methods and Materials

I sampled small mammals in the summers of 2009 and 2010. Sampling sessions in 2009 were 10 to 13 June, 17 to 20 June, and 24 to 27 June. Sessions in 2010 were weekly or biweekly from 20 May to 4 August. In most sessions I set at least one control grid (no edge), at least one high-contrast grid (grass-woods edge), and a low-contrast grid (grass-forbs edge). In some sessions I also set a woods-interior grid and/or a forbs-interior grid. Sessions were 3 consecutive nights (90 trapnights per grid) in 2009 and 2 nights (60 trapnights per grid) in 2010. Most grids were set as 6 rows of 5 traps (Figure 5). In 2010 some grids were set as 3 rows of 10 traps to sample more edge habitat.

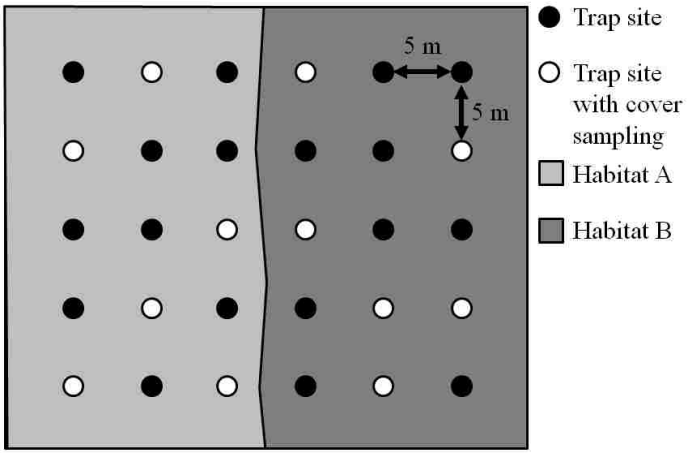

Figure 5. Layout of a typical trapping grid

In grids that contained an edge, 3 rows were set in each habitat (such that the boundary was between rows 3 and 4; Figure 5). In order to sample more edge habitat, 6 grids in 2010 were set at 3 rows of 10 traps rather than 6 rows of 5 traps. Grids were set ≥ 100 m apart within any given sampling session.

Small mammals were captured with Sherman folding traps (8 × 9 × 23 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida, USA) baited with crimped oats. Traps were checked each morning, left closed during the day, and collected after the last morning. Any trap that captured an animal was replaced with a clean trap, and all traps were cleaned and disinfected between sampling sessions (Yunger and Randa 1999). Animals were identified to species, weighed, assessed for sex and reproductive condition, and released at point of capture. Animals were marked with a numbered Monel™ ear tag (National Band and Tag Company, Newport, Kentucky) except for *Baiomys taylori* which are too small for ear tags (Sikes et al. 2011).

Plant cover was measured using a modification of the canopy-cover method of Daubenmire (1959) and Wilkins (1995) at 2 stations or 4 stations on each row in each grid (total of 12 trap stations per grid). Within a 0.1 m^2 quadrat I visually estimated the percentage of ground covered by 15 vegetation categories as being in 1 of 6 ranges: 0%, 1% to 5%, 6% to 25%, 26% to 50%, 51% to 75%, 76% to 95%, and 96% to 100%. The categories were: bluestem grasses at 10 cm, 25 cm, and 50 cm height above ground; secondary grasses at 10 cm, 25 cm, and 50 cm height; other grasses at 10 cm, 25 cm, and 50 cm height; forbs cover at 10 cm, 25 cm, and 50 cm height; and wooded cover at < 50 and ≥ 50 cm height. The bluestem grass category included little bluestem (*Schizachyrium scoparium*) and big bluestem (*Andropogon gerardii* Vitman). Secondary grass was

indiangrass (*Sorghastrum nutans*). The "other grass" categories include cover by buffalo grass (*Buchloe dactyloides* (Nutt.) Columbus), Johnson grass (*Sorghum halepense* (L.) Pers.), tall fescue (*Festuca arundinacea* Schreb.), switchgrass (*Panicum virgatum* L.), and others. Common forbs were dewberry (*Rubus* spp.), prairie bishop (*Bifora americana* Benth. & Hook. f. ex S. Watson), prairie parsley (*Polytaenia nuttallii* DC.), greenbriar (*Smilax bona-nox* L.), and poison ivy (*Toxicodendron radicans* (L.) Kuntze). Trees and woody shrubs found in or near wooded patches and drainages included osage orange (*Maclura pomifera* (Raf.) C. K. Schneid.), red mulberry (*Morus rubra* L.), smooth sumac (*Rhus glabra* L.), roughleaf dogwood (*Cornus drummondii* C. A. Mey), groundcherry (*Physalis* spp.), and eastern red cedar (*Juniperus virginiana* L.). For data analysis, the percentage of cover in a category was expressed as the midpoint of that range.

I used captures per 100 trapnights as a measure of small mammal relative abundance. Because rodent abundances were not normally distributed I used the Kruskal-Wallis one-way analysis of variance to test for differences in relative abundance between grid types. I also blocked the grids by week, such that the abundance of a species in an edge grid was only compared to the control grid in that week. The grids in a week were usually within the same section of Clymer Meadow, to eliminate macrohabitat effects. In week 5 of 2010 there was no control grid, so I compared those grids to the control grid nearest in space (grid II, sampled in week 9) in the same section of the preserve. I tested for within-block edge effects in 2010 using a one-sample two-tailed *t*-test; in 2009 there were too few blocks (3) to analyze edge responses in this way.

I measured edge contrast in two ways. The first measurement was qualitative: edges where grassland met dicot forb dominated habitat were considered "low contrast" edges, and edges between grassland and wooded patches were "high contrast." This distinction is based on ground cover. At these low contrast edges, habitat shifts from dense grass to grass intermingled with forbs. At high contrast edges, habitat shifts from dense grass to tree cover, with most ground bare or covered with sparse forbs and shrubs.

The second approach was more quantitative. I derived 6 quantitative measures of habitat contrast from vegetation data. The goal of these measures was to describe how much difference there was between the two habitats that met in a grid. Grids without edges would contain less overall variation in plant cover and would be expected to have lower values of the contrast metric. The metrics I tested were: 1) sum of Bray-Curtis distance matrix for every plant cover measurement within a grid (BCSUM); 2) sum of Bray-Curtis distance matrix for plant cover measurements from opposite ends of a grid (BCEND); 3) sum of Euclidean distance matrix for every plant cover measurement within a grid (EUSUM); 4) sum of Euclidean distance matrix for plant cover measurements from opposite ends of a grid (EUEND); 5) mean of Shannon diversity indices (MacArthur and MacArthur 1961) from plant cover measurements within a grid (SHMN); and 6) standard error of Shannon diversity indices from plant cover measurements within a grid (SHSE). A script in R was used to calculate these indices from vegetation data (Appendix). I used Kruskal-Wallis tests to evaluate whether each measure of contrast differed between treatment types. Negative binomial general linear models in the R package MASS (Venables and Ripley 2002) were used to model rodent

response to habitat contrast. All analyses were performed using R version 2.13.1 (R Development Core Team 2011).

Results

2009 Sampling Season

I sampled 17 grids in 2009 in 3 sampling sessions. I sampled 3 control grids (no edge), 4 grass-forb edge grids (low-contrast), 7 grass-forest edge grids (high contrast), 1 forbs interior grid, 1 grid dominated by small trees (*Cornus* spp. and *Physalis* spp.), and 1 forest interior grid (Table 1). Total sampling effort was 1530 trapnights. I captured 4 *B. taylori*, 12 *N. floridana*, 14 *P. leucopus*, 39 *P. maniculatus*, 11 *R. fulvescens*, and 369 *S. hispidus* (Table 1). Overall capture rate was 29.3 captures per 100 trapnights ± 5.1 SE.

I only attempted to analyze the 3 most abundant species. There was no significant effect of treatment for *P. maniculatus* (Kruskal-Wallis $\chi^2 = 2.66$, 2 df, $P = 0.26$) or for *R. fulvescens* (Kruskal-Wallis $\chi^2 = 2.34$, 2 df, $P = 0.31$). There was a weak effect of treatment on *S. hispidus* abundance (Kruskal-Wallis $\chi^2 = 5.3$, 2 df, $P = 0.07$). I suspected that one grid (grid C) might have exerted disproportionate influence on this test because abundance was very low in this grid compared to other control grids (overall capture rate 3.3 captures per 100 trapnights vs. 22.2 and 16.7 captures per 100 trapnights). When this grid was removed, the treatment effect on *S. hispidus* was significant (Kruskal-Wallis $\chi^2 = 6.66$, 2 df, $P = 0.04$). With grid C removed, there was still no significant treatment effect on abundance of *P. maniculatus* (Kruskal-Wallis $\chi^2 = 2.15$, 2 df, $P = 0.34$) or *R. fulvescens* (Kruskal-Wallis $\chi^2 = 1.69$, 2 df, $P = 0.43$).

Table 1. Mean (± SE) relative abundance (captures per 100 trapnights) of 6 small mammal species in trapping grids at Clymer Meadow in 2009

Treatment	*Baiomys taylori*	*Neotoma floridana*	*Peromyscus leucopus*	*Peromyscus maniculatus*	*Reithrodontomys fulvescens*	*Sigmodon hispidus*
All	0.3 ± 0.1	0.8 ± 0.3	0.9 ± 0.5	2.6 ± 0.6	0.7 ± 0.3	24.1 ± 5.2
Control	0.4 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	1.5 ± 1.5	0.0 ± 0.0	30.0 ± 14.8
Low contrast	0.3 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	1.1 ± 0.5	0.6 ± 0.6	36.7 ± 10.7
High contrast	0.3 ± 0.2	1.4 ± 0.6	1.6 ± 0.9	3.2 ± 0.9	0.6 ± 0.2	11.4 ± 6.0
Forbs interior	0.0	0.0	0.0	1.1	3.3	38.9
Small trees	0.0	0.0	0.0	6.7	2.2	50.0
Woods	0.0	3.3	4.4	4.4	0.0	4.4

When only tallgrass habitats were considered, there was no effect of treatment on abundance of *P. maniculatus* (Kruskal-Wallis $\chi^2 = 1.21$, 2 df, $P = 0.55$), *R. fulvescens* (Kruskal-Wallis $\chi^2 = 0.61$, 2 df, $P = 0.74$), or *S. hispidus* (Kruskal-Wallis $\chi^2 = 3.09$, 2 df, $P = 0.21$).

Contrast metrics were consistent descriptors of habitat edges but were poor predictors of rodent diversity. Kruskal-Wallis tests showed that the distance matrix-based metrics, but not the Shannon index-based metrics, were significantly different between treatments (Table 2). All four distance matrix-based metrics were generally higher in what I had designated high-contrast grids and lowest in control (no edge present) grids (Figure 6); the metrics based on the Shannon index showed no clear pattern. Low-contrast grids had contrast values intermediate to the other treatments but there was considerable intergradation (Figure 6).

Table 2. Summary data for six contrast metrics ($\bar{x} \pm$ SE) calculated from 2009 plant cover data. The χ^2 statistic and *P* value are for a Kruskal-Wallis test with 2 df for effect of treatment on the metric value

Metric	Control	Low contrast	High contrast	χ^2	*P*
Bray-Curtis, all samples	23.0 ± 2.9	38.8 ± 2.0	40.6 ± 2.8	9.63	0.008
Bray-Curtis, end rows	2.1 ± 0.3	3.8 ± 0.2	4.0 ± 0.2	10.23	0.006
Euclidean, all samples	4261 ± 439	6022 ± 497	6235 ± 585	5.37	0.07
Euclidean, end rows	390.8 ± 62.3	524.0 ± 69.1	626.2 ± 59.5	6.18	0.05
Shannon index, mean	1.5 ± 0.1	1.3 ± 0.1	1.3 ± 0.1	0.79	0.67
Shannon index, SE	0.06 ± 0.01	0.08 ± 0.01	0.10 ± 0.01	7.63	0.02

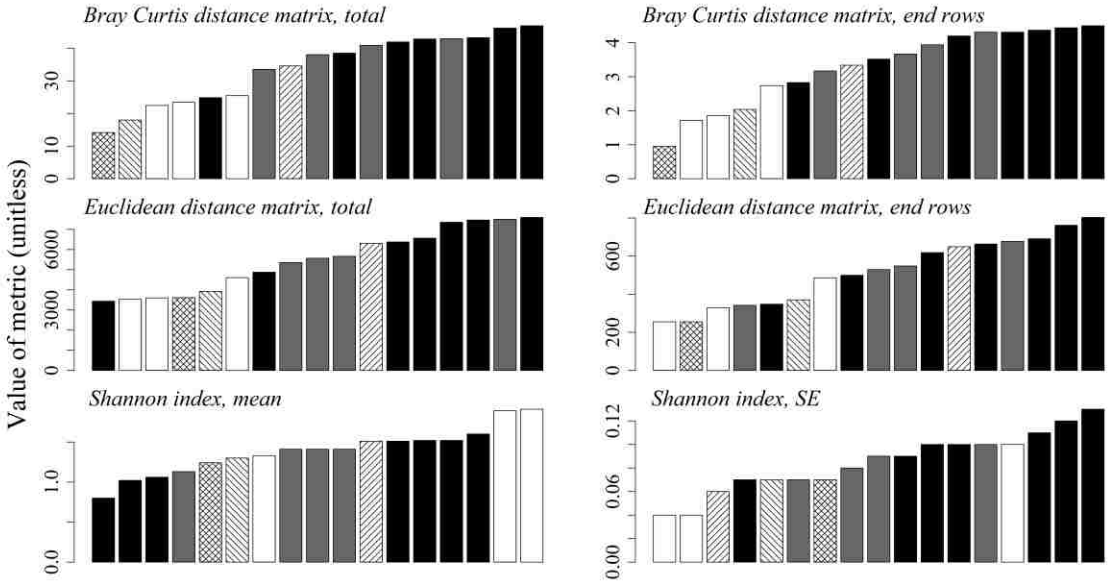

Figure 6. Six contrast metrics applied to plant cover data from 2009. White bars are grids without edges (control), grey bars are grids with grass-forbs edges (low-contrast), and black bars are grids with grass-wooded edges (high-contrast). Hatched bars are dicot forbs interior (▨), short trees interior (*Cornus* and *Physalis* spp; ▧), and a wooded drainage interior (⊠).

Negative binomial general linear models showed that only the mean Shannon index of plant cover diversity was a significant predictor of *S. hispidus* abundance (Table

3). This model predicted that *S. hispidus* abundance increases with increasing diversity in plant cover within a grid (Figure 7). The metrics based on distance matrices were not significant predictors of *S. hispidus* abundance.

Table 3. Numerical details of negative binomial general linear models of *S. hispidus* abundance explained by the contrast metrics

Year	Metric	Term	Estimate ± SE	*z*	*P*
2009	Shannon index, mean	Intercept	–1.15 ± 1.19	–0.97	0.33
		Metric	2.98 ± 0.83	3.58	< 0.01
2010	Bray-Curtis, all samples	Intercept	–2.36 ± 1.59	–1.48	0.14
		BCSUM	0.09 ± 0.04	2.05	0.04
	Bray-Curtis, end rows	Intercept	0.48 ± 1.05	0.46	0.65
		BCEND	0.15 ± 0.30	0.49	0.63
	Euclidean, all samples	Intercept	–2.04 ± 1.22	–1.67	0.09
		EUSUM	0.0004 ± 0.0002	2.36	0.02
	Euclidean, end rows	Intercept	0.17 ± 0.92	0.19	0.85
		EUEND	0.001 ± 0.001	0.89	0.37
	Shannon index, mean	Intercept	–1.79 ± 2.11	–0.86	0.39
		SH.MN	1.87 ± 1.47	1.27	0.20
	Shannon index, SE	Intercept	1.01 ± 1.03	0.98	0.33
		SH.SE	–1.51 ± 11.24	–0.13	0.89

2010 Sampling Season

I sampled 51 grids at Clymer Meadow in 2010. I sampled 17 control grids, 11 low contrast grids, and 23 high contrast grids. Based on high abundances found in 2009, I decided to reduce sampling period from 3 to 2 consecutive nights. Total sampling effort

in 2010 was 3060 trapnights. I captured 2 *B. taylori*, 3 *M. musculus*, 1 *N. floridana*, 6 *P. leucopus*, 17 *P. maniculatus*, 10 *R. fulvescens*, and 90 *S. hispidus* (Table 4).

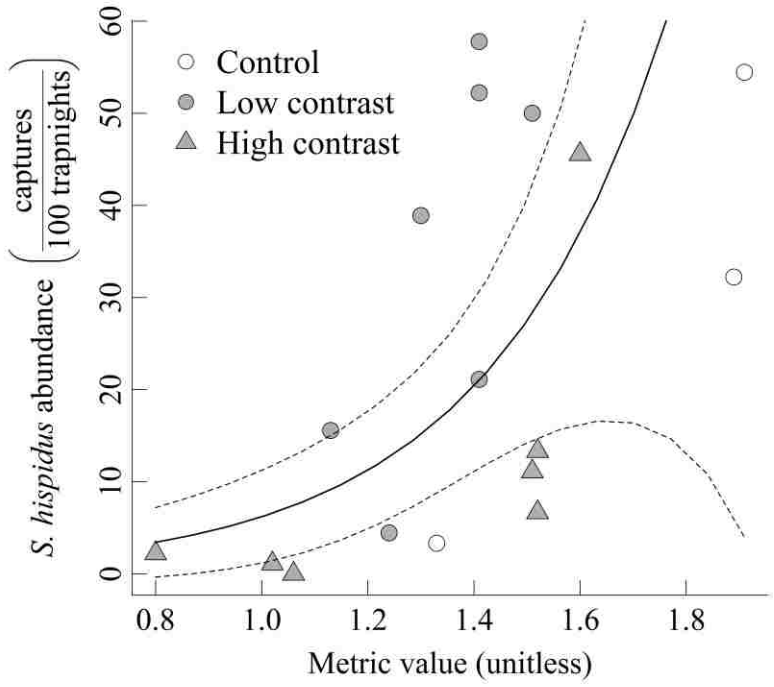

Figure 7. Predictions (± 2 SE) of a negative binomial GLM of *S. hispidus* abundance with the mean Shannon index contrast metric

Rodent abundance per grid was significantly smaller in 2010 (3.4 ± 0.6 captures per 100 trapnights) than in 2009 (29.3 ± 5.1 captures per 100 trapnights; two-tailed t = 5.05, 16.51 df, $P < 0.01$). Twenty of the 51 grids experienced no captures and every species was captured in < 50% of grids. As in 2009, I analyzed treatment effect only for the most abundant species (*P. maniculatus*, *R. fulvescens*, and *S. hispidus*). There was no significant effect of grid type for *P. maniculatus* (Kruskal-Wallis $\chi^2 = 0.63$, 2 df, P = 0.73), *R. fulvescens* (Kruskal-Wallis $\chi^2 = 2.23$, 2 df, $P = 0.33$), or *S. hispidus* (Kruskal-Wallis $\chi^2 = 1.14$, 2 df, $P = 0.57$).

Table 4. Mean (± SE) relative abundance (captures per 100 trapnights) of 6 small mammal species in trapping grids at Clymer Meadow in 2010

Species	All grids	Control	Low contrast	High contrast
Baiomys taylori	0.1 ± 0.1	0.0 ± 0.0	0.2 ± 0.2	0.1 ± 0.1
Mus musculus	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1
Neotoma floridana	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1
Peromyscus leucopus	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.2
Peromyscus maniculatus	0.3 ± 0.1	0.3 ± 0.2	0.5 ± 0.2	0.6 ± 0.3
Reithrodontomys fulvescens	0.4 ± 0.2	0.1 ± 0.1	0.5 ± 0.2	0.6 ± 0.3
Sigmodon hispidus	2.4 ± 0.6	3.6 ± 1.3	2.6 ± 1.8	1.5 ± 0.5

When grids were analyzed by blocks (Figure 8), I found that *S. hispidus* responded weakly negatively to high contrast edges (two-tailed $t = -1.76$, df = 13, $P = 0.10$) and did not respond to low-contrast edges (two-tailed $t = -1.41$, 13 df, $P = 0.18$). *Peromyscus maniculatus* did not respond to high contrast edges (two-tailed $t = -0.43$, 13 df, $P = 0.67$) or low contrast edges (two-tailed $t = 0$, 13 df, $P > 0.99$). *R. fulvescens* did not respond to high contrast edges (two-tailed $t = 1.24$, 13 df, $P = 0.24$) or low contrast edges (two-tailed $t = 1.43$, 13 df, $P = 0.17$).

Contrast metrics were consistent descriptors of habitat edges but were poor predictors of rodent diversity. Kruskal-Wallis tests showed that the distance matrix based metrics were significantly different between treatments (Table 5). All four distance matrix-based metrics were generally higher in what I had designated high-contrast grids and lowest in control (no edge present) grids (Figure 9). The metric based on the mean Shannon index ranked the grids in roughly opposite order (Figure 9).

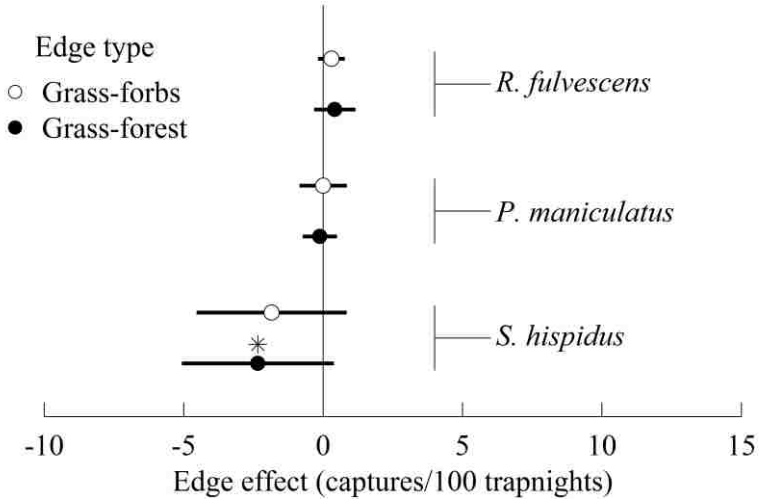

Figure 8. Within-block edge effects ($\bar{x} \pm 2$ SE) at Clymer Meadow in 2010. Asterisk denotes effect is significantly different from 0

Table 5. Value of contrast metrics ($\bar{x} \pm$ SE) in each treatment at Clymer Meadow in 2010. The χ^2 statistic and *P* value are for a Kruskal-Wallis test with 2 df for effect of treatment on the metric value

Metric	Control	Low contrast	High contrast	χ^2	*P*
Bray-Curtis, all samples	31.60 ± 1.52	34.65 ± 2.15	39.62 ± 1.34	16.15	0.0003
Bray-Curtis, end rows	2.82 ± 0.24	3.15 ± 0.31	3.91 ± 0.11	10.77	0.0045
Euclidean, all samples	4866 ± 310	5577 ± 279	6758 ± 294	14.51	0.0007
Euclidean, end rows	436 ± 43	505.41 ± 49.26	695.24 ± 19.88	15.41	0.0004
Shannon index, mean	1.48 ± 0.07	1.37 ± 0.07	1.39 ± 0.03	5.78	0.0556
Shannon index, SE	0.08 ± 0.00	0.10 ± 0.01	0.09 ± 0.01	2.86	0.2399

Negative binomial general linear models showed that the metrics using the sum of a distance matrix of all vegetation samples within a grid were significant predictors of *S. hispidus* abundance (Table 3). A likelihood ratio test showed that these models were not significantly different in performance. The difference in deviance between the BCSUM and EUSUM models was 1.74 and follows a Chi-square distribution with 1 df ($P > 0.99$).

These models showed that *S. hispidus* abundance increased slightly with increasing variability in plant cover within a grid (Figure 10). The metrics based on the Shannon index were not significant predictors of *S. hispidus* abundance.

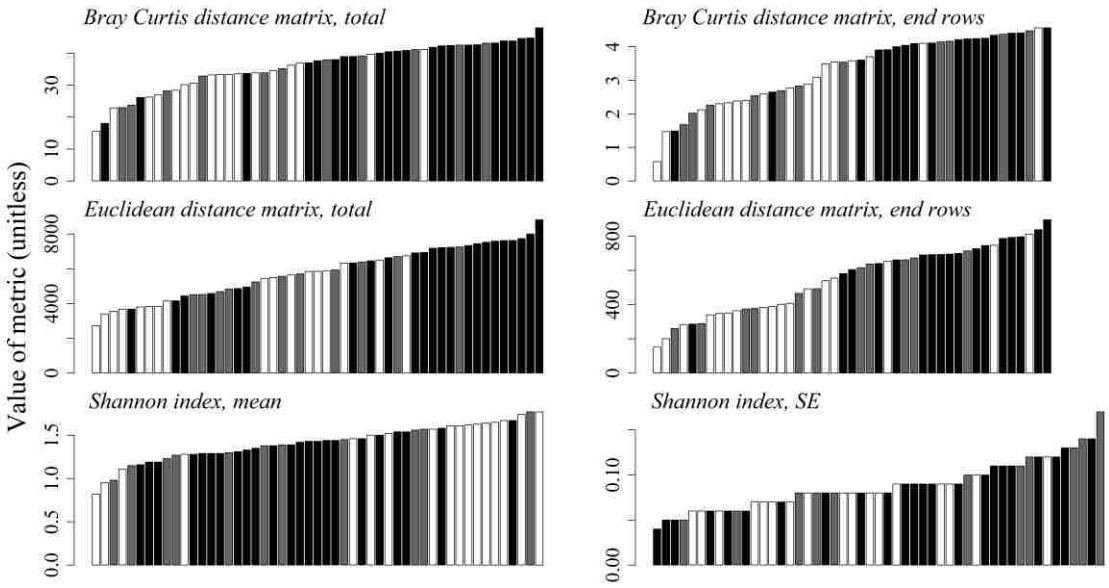

Figure 9. Six contrast metrics applied to plant cover data from 2010. White bars are grids without edges (control), grey bars are grids with grass-forbs edges (low-contrast), and black bars are grids with grass-wooded edges (high-contrast)

Discussion

Pilot sampling was useful in discovering flaws in my original experimental design. The small number of grids sampled in 2009 showed that studying edge effects on prairie landscapes would require many sampling grids, and that each treatment should contain as many replicates as possible. Therefore, attempting to locate a sufficient number of "interior" grids for every habitat on a landscape might not be feasible if the landscape is small. It also became apparent that year-to-year variation in capture rates could have a profound influence on my conclusions. Very high capture rates in 2009 and very low capture rates in 2010 both made it difficult to analyze differences between

experimental treatments. Following the 2010 field season I decided to find a new, much larger study location where there would be space for sufficient replication and rodent densities that were somewhere between intractably low (2010 data) and intractably high (2009 data).

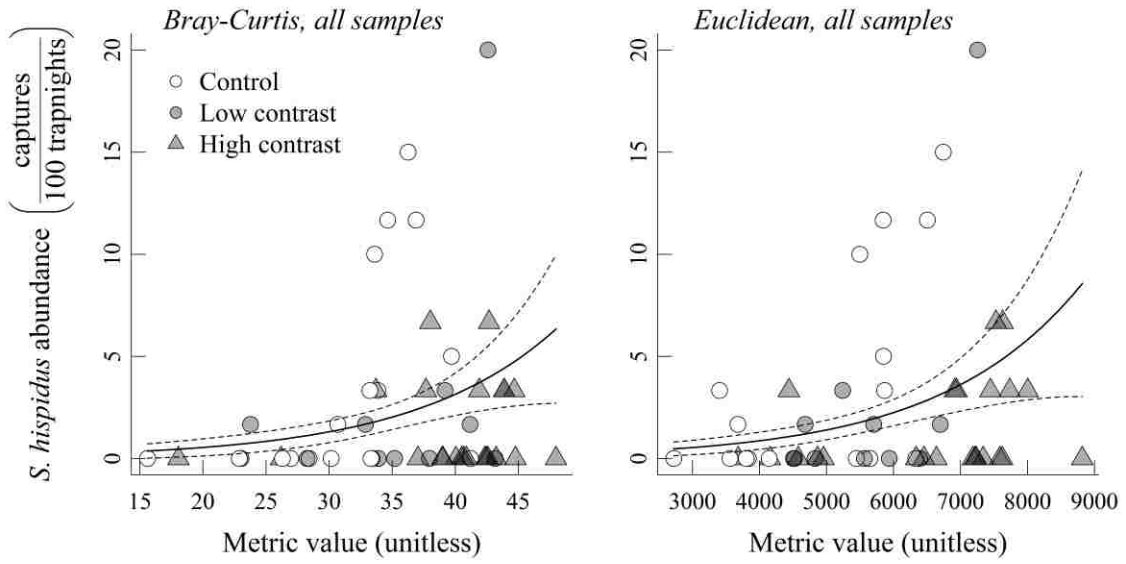

Figure 10. Predictions and 95% CI of negative binomial generalized linear models of *S. hispidus* abundance vs. two contrast metrics

The results of pilot sampling were inconclusive. In both years I found no evidence of edge effects in *P. maniculatus* or *R. fulvescens*. The lack of edge effects in *P. maniculatus* was not entirely surprising. This species is often regarded as a habitat generalist, able to utilize many different habitat types (Wolff et al. 1985; Wywialowski 1987). The breadth of the niches exploited by this species may render habitat variation at small spatial scales irrelevant to *P. maniculatus*. Lack of edge responses in *R. fulvescens* was more surprising. This species is strongly associated with grassland habitats containing forbs (Spencer and Cameron 1982) and was expected to be less abundant near

wooded edges. Lack of an edge effect may have been an artifact of low capture rates and the abundance of zeroes (no captures) in the dataset.

Sampling in 2009 found weak edge effects in *S. hispidus*. Cotton rats were less abundant near the edges of wooded patches than in tallgrass interior or tallgrass-forbs edges. Cotton rat abundance was higher in grids where tallgrass abutted dicot forb-dominated habitat, but the number of control grids was too small ($n = 3$) to test for significance. Higher abundance at tallgrass-forbs edges may have been caused by the increased nutritional content of dicot forbs compared to grasses. Dicot forbs are higher in digestible carbohydrate, protein, lipids, and minerals than C_4 grasses such as those found at Clymer Meadow (Randolph et al. 1991, Randolph et al. 1995). The importance of these plants will be explored in Chapter 4. In the context of the resource distribution hypothesis (Ries and Sisk 2004), increased abundance at low contrast edges is caused by resource complementarity between tallgrass habitat and forb-dominated habitat. The most important resources in question are probably cover and refuge (tallgrass habitat; Goertz 1964) and high-quality nutrition (forb-dominated habitat). In this framework, the high-contrast edges either present supplementary resources or a boundary between suitable and unsuitable habitat. Both situations are expected to cause negative edge responses.

In 2010, cotton rat abundance was highest in tallgrass interior grids and lowest near wooded edges, but the differences in abundance between treatments were nonsignificant. If abundances at the tallgrass-forbs edge grids truly were intermediate between the other grid types, this is a pattern that differs between the years. When abundances were high in 2009, cotton rat abundances were higher at low-contrast edges

than tallgrass interiors; this pattern was reversed in 2010 when abundances were low. If real this reversal would suggest that tallgrass-forbs habitats are suboptimal for cotton rats; being preferentially occupied only when tallgrass habitat is unavailable. The fact that abundance near high-contrast edges was consistently lowest during both the high-abundance year and the low-abundance year suggests that these habitats are sub-optimal for cotton rats and that any response to this edge is likely to be a habitat-matrix effect (Lidicker and Peterson 1999) rather than an effect of resource distribution (Ries and Sisk 2004). This idea will be explored in Chapter 5.

The notion of using a metric of edge contrast, composited from measures of plant cover on either side of the grid, was problematic. Two approaches were tried. The distance matrix approach assumed that the greater the difference between the habitats at an edge, the greater the distances would be found in a distance matrix of plant cover samples within a grid that crossed the edge. The other approach assumed that greater differences in habitat at an edge would mean greater heterogeneity of plant cover, with heterogeneity expressed as the Shannon index with categories or plant cover as species. Several variants of each approach were applied to the plant cover data and I found that the distance matrix-based approaches were much more likely to show a difference between the 3 treatments (grass-interior, low-contrast, and high-contrast). I also found that, as predicted, the distance matrix-based approaches generally assigned higher values to grass-wooded edges than to control grids (Figure 6, Figure 9) and that the low-contrast grids were not concentrated near the center of any of the scales. Even the best-performing contrast metric, EUSUM, had some intergradation of the treatments (Figure 6, Figure 9).

The lack of complete separation of treatment types by any contrast metric could have been caused by several factors. First, the metrics were calculated from plant cover data that included 3 separate taxonomic categories of grass cover, but the grid locations were chosen before plant cover was measured in that much detail. Habitat perceived as "grass" at a distance could have contained much diversity. Second, variation within treatments could have distorted some grids' metric values. For example, many wooded patches at Clymer Meadow contain large stands of river oats (*Chasmanthium latifolium* (Michx.) H. O. Yates), which would have been recorded as "other grass." These grass-containing wooded patches would have had smaller values in their distance matrices, and thus smaller metric values. One way to improve this method might be to weight some plant cover variables more than others, particularly the most dominant types. At Clymer Meadow, those might be bluestem grasses, dicot forbs, and tree cover. Finally, it may not be realistic to expect perfect correspondence between a qualitative assessment of a location (e.g., "This is a low contrast edge.") and a more quantitative expression of cover diversity at that location.

While some of the metrics could adequately characterize the presence or contrast of an edge within a sampling grid, there was almost no relationship between small mammal abundance and any contrast metric. Small mammals at Clymer Meadow did vary with plant cover and in the high abundance year (2009) one species (*S. hispidus*) responded differently to the two edge types. In the low abundance year (2010), there was no such edge effect, but that could have been caused by the high frequency of zeros in the dataset. In both years the distance matrix-based contrast metrics did differ between grid types in the way I had expected, but these same metrics were poor predictors of *S.*

hispidus abundance. In both years *S. hispidus* responded to contrast in the opposite manner as expected: abundance increased with contrast. This is paradoxical, because when contrast was analyzed as a factor, *S. hispidus* abundance was lower in the wooded edge grids, which had high contrast scores. For the edge types encountered in tallgrass prairie, qualitative classification may be sufficient for understanding small mammal edge responses.

After the summer 2010 sampling season I decided to abandon Clymer Meadow and find a new study site. Criteria for the new study site were: 1) larger than Clymer Meadow; 2) higher small mammal abundance than observed in 2010; and 3) several habitat types present, with clear boundaries between them. I chose the LBJ National Grasslands, near Decatur, Wise County, Texas. The following chapters are derived from sampling in 2011 at the LBJ National Grasslands.

Acknowledgments

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CHAPTER THREE

Effects of Plant Cover and Microhabitat Heterogeneity on Three Grand Prairie Small Mammals

Abstract

I sampled small mammal abundance and microhabitat associations at the Lyndon B. Johnson National Grassland, an 8218 ha Grand Prairie preserve near Decatur, Wise County, Texas. I recorded 5 rodent species at the preserve: hispid cotton rat (*Sigmodon hispidus*), white-footed mouse (*Peromyscus leucopus*), deer mouse (*P. maniculatus*), fulvous harvest mouse (*Reithrodontomys fulvescens*), and hispid pocket mouse (*Chaetodipus hispidus*). *Sigmodon hispidus* was most abundant in microhabitats with dense grass cover, and *P. maniculatus* was most abundant in trapping grids with intermediate forb and bare ground cover and trees. *Chaetodipus hispidus* was associated with intermediate levels of grass cover. In addition, *S. hispidus* avoided heterogeneous habitats, while *P. maniculatus* preferred them. The contrasting responses to habitat heterogeneity reflect the grassland specialization of *S. hispidus* and generalist habits of *P. maniculatus*. Though my findings generally agree with previous studies, these observations suggest that plant cover heterogeneity at small spatial scales (tens of meters) exerts strong influence on rodent abundance and diversity.

Introduction

Habitat selection, or the nonrandom association of organisms with spaces where they acquire resources, is reflective of both short-term fitness and evolutionary history (Martin 1998; Morris 2003) and thus can drive population and community dynamics in

the short term and evolutionary trends over long time spans. Optimal habitat for a species may be similar across its entire range or can vary with factors such as season, geography, sex, reproductive status, resource availability, population size, predation, and interspecific competition (Bowers 1986). Thus, observational studies in many ecoregions and situations are necessary for thorough understanding of a species' ecology.

Small mammals (body mass ≤ 1 kg) are found in most terrestrial habitats and affect their environments in direct and indirect ways (Hayward and Phillipson 1979). Direct effects include herbivory and seed predation (Batzli and Pitelka 1970; Hulme 1996), insectivory (Churchfield et al. 1991), and deposition of N-rich feces and urine (Clark et al. 2005). Indirect effects include alteration of plant community composition (Weltzin et al. 1997; Brewer and Rejamánek 1999; DeMattia et al. 2004; Bagchi et al. 2006) and edaphic effects through burrowing (Weltzin et al. 1997). Small mammals are an important food source for many medium-sized and large predators (Cameron and Spencer 1981). Thus, understanding the drivers of small mammal abundance can be useful in land management decision making.

Small mammal habitat selection is usually studied at either the macrohabitat or the microhabitat level, although there is some inconsistency in how those terms are used (Jorgensen 2004). Morris (1987) defined macrohabitat as the spatial area in which individuals perform all their biological functions and microhabitat as being subsets of a macrohabitat defined by environmental variables that affect individual behavior. In this paradigm, habitat associations could be interpreted as the association of a species with a macrohabitat type or the preference within a macrohabitat for certain microhabitats. This definition is useful because it allows the distinction between macrohabitat and

microhabitat to be species-specific and offers a framework for interpreting habitat associations at both scales. Researchers must be cautious because evidence for microhabitat partitioning may actually be evidence for a mixture of macrohabitat and microhabitat selection (Morris 1984) or may be confounded by analysis at inappropriate spatial scales (Jorgensen 2004). There is considerable evidence that small mammal habitat associations vary with spatial scale and that habitat variation at larger scales might be more appropriate for predicting abundance of generalist species (Morris 1984, 1987; Jorgensen and Demarais 1999a; Orrock et al. 2000). For example, Morris (1996) found that at small spatial scales specialists such as red-backed voles (*Clethrionomys gapperi*) and deer mouse (*P. maniculatus*) could outcompete more generalist chipmunks (*Tamias amoenus* J. A. Allen 1890), but chipmunks persisted by responding to habitat at a larger spatial scale. In landscapes where *Peromyscus* species are generalists, they tend to respond to habitat at larger scales and coarser grain than specialist species (Adler and Wilson 1987; Kolasa 1989). Jorgensen (2004) also found great inconsistency among small mammal microhabitat studies in quantification of habitat variables and selection of spatial scale. Another factor in whether a species is a specialist or generalist is whether the species depends on a few food sources or on many (Begon et al. 2006).

Small mammal use of microhabitats is driven primarily by diet (Cameron and Spencer 2008) and by physical habitat characteristics such as structural complexity and space (Carey and Wilson 2001). Which driver is more important usually depends on a species' life history. Species that subsist largely on a single kind of food source will be more abundant when food is abundant. Abundances of species that utilize a variety of food types tend to vary more with physical habitat characteristics than any particular food

source. The relative importance of dietary and physical resources may be altered by population density, competition, and other factors.

I investigated habitat associations of small mammals at a mixed-grass prairie preserve in northern Texas. Based on previous literature, I predicted that abundance of the largely foliovorous hispid cotton rat (*Sigmodon hispidus*) would correlate negatively with woody plant cover and bare ground, and positively correlated with grassy ground cover (Cameron and Spencer 1981; Wilkins 1995; Kaufman and Kaufman 1997; Hanchey and Wilkins 1998; Jones et al. 2003) and dicot forbs (i.e., herbaceous ground cover; Cameron and Spencer 2008). Because *S. hispidus* has such a strong association with grassland habitat and depends primarily on grasses for food and shelter, I predicted that cotton rat abundance would be negatively correlated with habitat heterogeneity.

I hypothesized that deer mice (*Peromyscus maniculatus*), a generalist species with a diverse diet, would respond positively to bare ground and non-grassy vegetation (Snyder and Best 1988; Kaufman and Kaufman 1990; Kaufman and Kaufman 1997). Because *P. maniculatus* is known to occur in a wide range of structurally complex habitats and exploits a variety of food sources, I predicted that deer mouse abundance would be positively correlated with habitat heterogeneity (Carey and Wilson 2001). I hypothesized that abundance of hispid pocket mice (*Chaetodipus hispidus* (Baird 1858)), a granivorous heteromyid rodent, would be associated with intermediate levels of all categories of ground cover and higher habitat heterogeneity (Paulson 1988; Clark et al. 1998; Jones et al. 2003).

Study Site and Sampling Protocol

Small mammals were trapped at the Lyndon B. Johnson National Grasslands (LBJNG) near Decatur, Wise County, Texas (Figure 11). The LBJNG is an 8218 ha network of 67 managed units within the Cross Timbers EPA Level III ecoregion (Wilken et al. 2011). Eastern sections of the LBJNG are in the Grand Prairie (Level IV ecoregion 29d) and western sections fall within the Western Cross Timbers (Level IV ecoregion 29c; Griffith et al. 2007). The units range in size from 2 to 1201 ha. I sampled in 11 units within the Grand Prairie ecoregion (Figure 11).

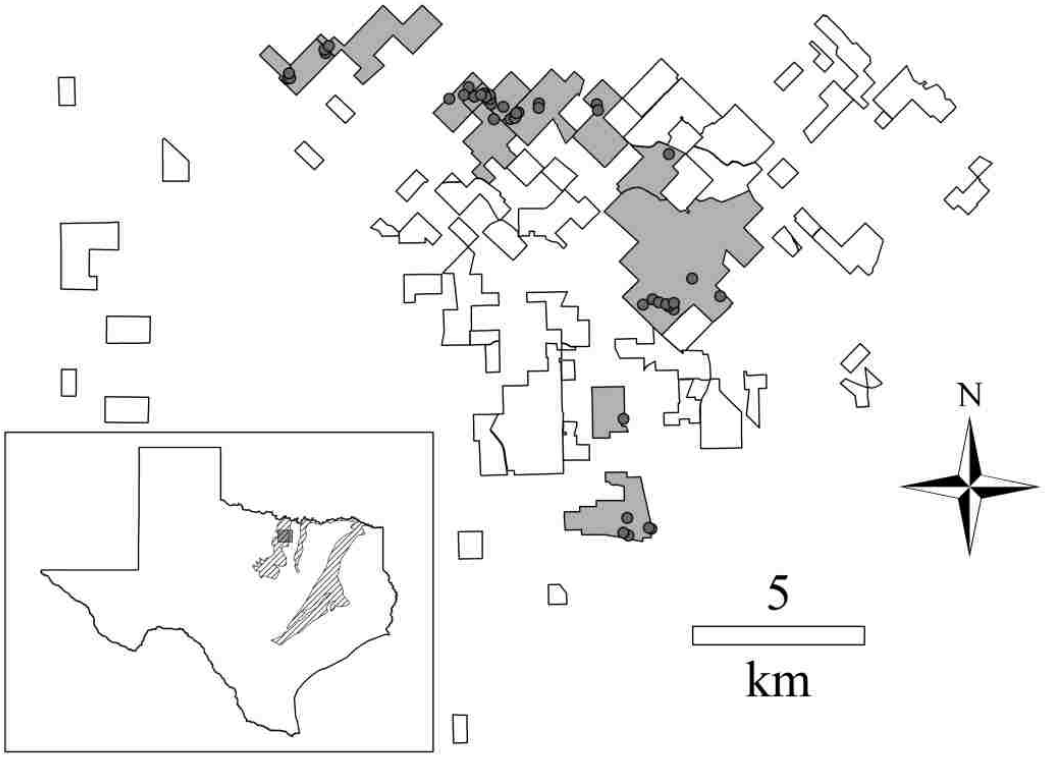

Figure 11. Eleven units (shaded) of the Lyndon B. Johnson National Grasslands near Decatur, Wise County, Texas (county shaded in inset) were sampled. Dots show location of sampling grids. Inset shows location of study site in Texas, and the Grand Prairie ecoregion (hatched area in inset)

Small mammals were sampled in 14 weekly trapping sessions from 3 May to 4 August 2011. In each session, I set 3 grids of 30 traps each for 3 consecutive nights. Forty two separate grids were sampled during the study. Grids were separated by > 100 m and I checked for spatial and temporal autocorrelation before treating grids as independent samples. Total trapping effort was 3777 trapnights (3780 trapnights were set, but several traps found damaged were not included in analyses). Sherman small mammal traps (8 × 9 × 23 cm) were set and baited with crimped oats within 3 h of sunset. Traps were checked within 2 h of sunrise, left closed during the day, and collected on the third morning. Captured animals were identified to species, weighed, assessed for sex and reproductive condition, and marked with an ear tag. I also took a blood sample of from cotton rats weighing ≥ 30 g (Chapter 4). All procedures involving animals were approved by the Baylor University Animal Care and Use Committee and in accordance with the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011). Sampling was carried out under Texas Parks and Wildlife Scientific Collection Permit SPR 0706–704 issued to K. T. Wilkins and United States Forest Service Special Use Permit LBJ006701 issued to N. S. Green.

I also sampled vegetation using a modification of the canopy-cover method of Daubenmire (1959) at 6 to 12 randomly selected trap stations per grid (Chapter 2). Within a 0.1 m^2 quadrat I estimated percentage of ground covered by 13 vegetation categories (Table 6) and tree cover. The bluestem categories are cover by the dominant grass, little bluestem (*Schizachyrium scoparium*). Other grass includes cover by Indian grass (*Sorghastrum nutans*), buffalo grass (*Buchloe dactyloides*), Johnson grass (*Sorghum halepense*), hairy grama (*Bouteloua hirsuta* Lag.), and others. For data

analysis, the percentage of cover in a category was expressed as the midpoint of that range, and the mean of all stations in a grid was used as the value for the whole grid. I added bluestem and other grass cover to obtain total grass cover at each height. I calculated the Shannon diversity index (H') of plant cover in each grid (MacArthur and MacArthur 1961) using variables in Table 6 as species to assess habitat heterogeneity.

Table 6. Summary of variables used for constructing generalized additive models (GAM) and generalized additive mixed models (GAMM) of rodent abundance

Variable	Definition	Minimum	Maximum	$\bar{x} \pm$ SE
Bare	Bare ground (%)	0	26.8	5.5 ± 1.1
Grass10	Total grass cover at 10 cm (%)	8.2	95.3	64.0 ± 3.7
Grass25	Total grass cover at 25 cm (%)	3.5	58.7	24.4 ± 2.2
Grass50	Total grass cover at 50 cm (%)	0	33.9	10.4 ± 1.3
Blue10	Bluestem cover at 10 cm (%)	5.1	93.8	58.6 ± 4.0
Blue25	Bluestem cover at 25 cm (%)	1.5	58.4	22.4 ± 2.2
Blue50	Bluestem cover at 50 cm (%)	0.0	33.8	9.5 ± 1.3
Other10	Other grass cover at 10 cm (%)	0.0	30.9	5.4 ± 1.0
Other25	Other grass cover at 25 cm (%)	0.0	11.1	2.0 ± 0.3
Other50	Other grass cover at 50 cm (%)	0.0	4.9	0.9 ± 0.2
Forb10	Forbs cover at 10 cm (%)	0.0	58.8	17.2 ± 2.2
Forb25	Forbs cover at 25 cm (%)	0.0	36.8	5.9 ± 1.2
Forb50	Forbs cover at 50 cm (%)	0.0	18.3	2.1 ± 0.7

Data Analysis

Exploratory analyses suggested that rodent abundances fit the negative binomial distribution (Ver Hoef and Boveng 2007). I used nonmetric multidimensional scaling and environmental vector fitting to determine which vegetation variables might be most useful for modeling rodent abundance (McCune and Grace 2002; Zuur et al. 2007). Scatterplot matrices and nonmetric multidimensional scaling were used to check for collinearity and other associations between explanatory variables to avoid inclusion of redundant environmental variables in models. Mantel tests with randomization were used to check for spatial and temporal autocorrelation in mammal abundances. Percentage cover by other grass, bare ground, and forbs were square-root transformed to alleviate severe skewness. The field-measured woody vegetation above 50 cm (i.e., tree canopy cover) was converted to a binary variable because most values were 0.

I chose an additive modeling approach because exploratory analyses found no clear linear dependence of any rodent species' abundance on plant cover variables. Additive models model nonlinearity in the response variable by applying a smoothing function to each explanatory variable (Wood 2006). Each smoothing function consumes degrees of freedom to fit a nonlinear relationship between the response and explanatory variable. More complex smoothing functions require more degrees of freedom. In each additive model I restricted the basis dimension of each smoother—a measure of complexity approximately equal to one less than degrees of freedom consumed—to 2 or 3 to avoid over-fitting the model to noise (Zuur et al. 2007). I used generalized additive mixed models (GAMMs) for *S. hispidus* and *P. maniculatus* because there was considerable variance in capture rate due to time (week of sampling season). I used

generalized additive models (GAMs) for *C. hispidus* because there was very little variance in week-to-week capture rate and no need for a random effect. Model selection process generally followed that of Zuur et al. (2009): I first found a close-to-optimal GAM of abundance, used this model to develop an optimal random effect structure, and then fine-tuned the fixed effect structure. Models were compared with the Quasi-Akaike's information criterion corrected for small sample size ($QAIC_c$) calculated by restricted maximum likelihood estimation (Zuur et al. 2009; Barton 2011).

Chaetodipus hispidus and *P. maniculatus* were usually present in small numbers, so I was confident selecting only one "best" model of abundance. For the more abundant *S. hispidus*, I report 3 models: 1) abundance vs. total grass cover; 2) abundance vs. bluestem and other grasses; and 3) abundance vs. non-grass ground covers. To aid interpretation of all models, I present predictions of each model of rodent abundance across the range of observed ranges of explanatory variables; in multivariate models predictions for each variable are made while holding other variables constant at their medians (Figures 12 to 14). All analyses were performed in R version 2.13.1 (R Development Core Team, 2011). I used package mgcv for additive modeling (Wood 2011), package vegan for calculating Shannon's index (Oksanen et al. 2011), and package MuMIn for calculating $QAIC_c$ scores (Barton 2011).

Results

Capture Summary

I captured 311 small mammals of 5 species: 233 *S. hispidus*, 37 *P. maniculatus*, 25 *C. hispidus*, 13 fulvous harvest mice (*Reithrodontomys fulvescens*), and 3 white-footed

mice (*P. leucopus*). Mean capture rate per grid was 8.2 ± 1.1 captures per 100 trapnights. Total capture rate ranged from 0 to 26.6 captures per 100 trapnights. I detected no spatial autocorrelation between grids with respect to rodent abundance (|Mantel's r| < 0.08, $P \geq 0.14$ for all species), nor temporal autocorrelation (|Mantel's $r| < 0.04$, $P \geq 0.26$ for all species).

Species Abundances

Sigmodon hispidus. Hispid cotton rats were detected in 29 of 42 trapping grids. Mean capture rate of cotton rats was 6.2 ± 1.1 captures per 100 trapnights, ranging from 0 to 26.6 captures per 100 trapnights. I fit 3 sets of generalized additive mixed models of cotton rat abundance using different sets of predictor variables. Each model used WEEK as a random effect, a log link function, and the negative binomial distribution. I did not include a random effect for space because there was already autocorrelation between the grids in time and space (Mantel's $r = 0.5619$, $P < 0.01$); i.e., sampling grids were more likely to be close to grids in the prior, same, or subsequent sampling session than they were to be close to grids in sessions farther away in time.

The total grass models described *S. hispidus* abundance as increasing with total grass cover at all heights, but the relationship was strongest at 50 cm (Table 7). This model had no patterns in residuals. The model predicted a linear increase in cotton rat abundance with increasing grass cover (Figure 12a).

All 9 possible combinations of grass by species models (3 heights available for both bluestem and other grasses) predicted cotton rat abundance increasing with bluestem coverage and decreasing with cover by other grasses (e.g., Figure 12b and 12c). The

model using bluestem grass cover at 50 cm and square-root transformed other grass cover at 25 cm had the greatest $QAIC_c$ weight (0.19), but all models were included in the 95% confidence set of models (Table 7).

Table 7. Numerical details of generalized additive mixed models of cotton rat (*Sigmodon hispidus*) abundance. $QAIC_c$ values cannot be directly compared between models because models are not nested. $QAIC_c$ is Quasi-Akaike Information Criterion for small samples, *r* is Pearson correlation coefficient between fitted values and observed values, estimate is estimate of parametric component, T.S. is test statistic for each parametric component (*t*) or smoother (*F*), EDF is estimated degrees of freedom used by smoother, and *P* is the significance value for the test statistic

Model	$QAIC_c$	*r*	Estimate ± SE	T.S.	EDF	*P*
Total grass	39.9	0.39				
Intercept			1.57 ± 0.22	7.19		< 0.01
Grass50				7.02	1.00	0.01
Grasses by spp.	48.7	0.41				
Intercept			1.43 ± 0.21	6.86		< 0.01
Blue50				8.63	1.00	< 0.01
Other25*				6.71	1.72	< 0.01
Non-grass model	24.9	0.54				
Intercept			1.33 ± 0.19	6.86		< 0.01
Bare*				18.09	1.00	< 0.01
Model by H′	18.4	0.39				
Intercept			1.52 ± 0.24	6.32		< 0.01
H′				11.01	1.00	< 0.01

* Variable is square-root transformed

Forb cover was not a significant predictor of abundance in any candidate model. In the best non-grass model, cotton rat abundance was highest in grids with high and low values of bare ground (Table 7, Figure 12d). The effect of tree cover was significant at $P = 0.054$. Because the increase in abundance at high values of bare ground was contrary to expectations and to literature, I suspected that the three sampling grids with highest bare ground (white symbols in Figure 12d) may have distorted the relationship. Without these grids, cotton rat abundance decreased with increasing bare ground and there was no significant effect of tree cover or forb cover (Table 7; Figure 12d). Non-grass models with forbs were omitted when calculating global model $\hat{c}$ for the calculation of $QAIC_c$ because models including forbs cover failed to converge on a stable solution.

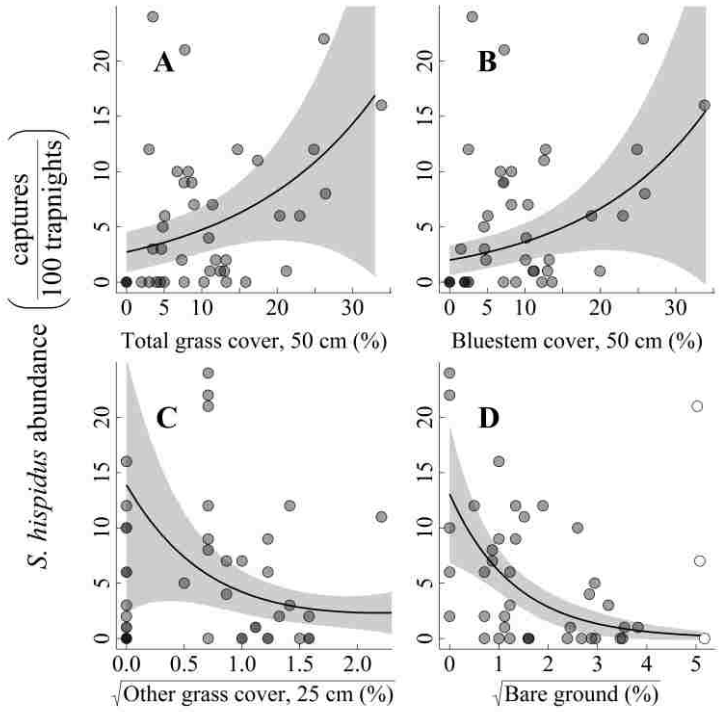

Figure 12. General additive mixed model predictions (and 95% CI) of cotton rat (*Sigmodon hispidus*) abundance. A. Total grass model; B. and C. Bluestem and other grass model; D. Non-grass cover model. Three sampling grids (white symbols) were removed from analysis of non-grass cover types (see text). Points show observed values

Peromyscus maniculatus. Deer mice were detected in 12 of 42 trapping grids. Mean capture rate of deer mice was 1.0 ± 0.3 captures per 100 trapnights, ranging from 0 to 11.1 captures per 100 trapnights. Abundance of *P. maniculatus* was described by a GAMM using forb cover at 25 cm, bare ground, and tree presence as predictor variables, a log link function, WEEK as a random effect, and the negative binomial distribution (Table 8). Grass cover was not included in the *P. maniculatus* model because it was either nonsignificant or, when significant, predicted unrealistically large abundances (e.g., ≫ 1000 captures per 100 trapnights). The final *P. maniculatus* model predicted higher abundance at mid-range values of forbs cover and bare ground, and when trees were present (Figure 13).

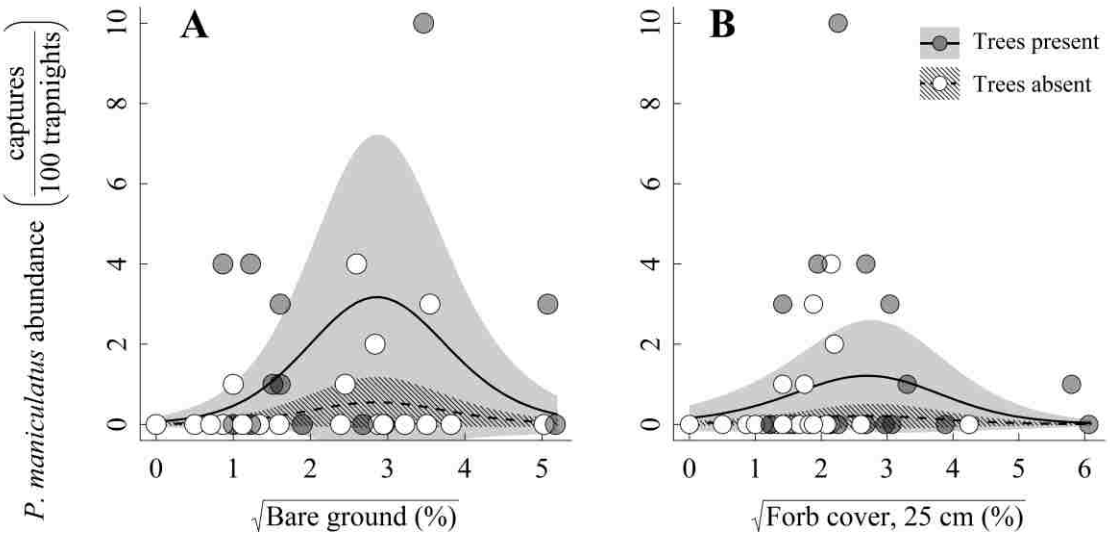

Figure 13. General additive mixed models of deer mice (*Peromyscus maniculatus*) abundance. Abundance was highest at intermediate values of (A) bare ground and (B) forb cover. Points show observed values; lines show model predictions, and shaded regions are 95% CI. Note that independent variables are square-root transformed

Table 8. Numerical details of the generalized additive mixed models (GAMM) explaining deer mouse (*Peromyscus maniculatus*) abundance. $QAIC_c$ is Quasi-Akaike Information Criterion for small samples, *r* is Pearson correlation coefficient between fitted values and observed values, estimate is estimate of parametric component, T.S. is the test statistic for parametric component (*t*) or smoother (*F*), EDF is estimated degrees of freedom used by the smoother, and *P* is the significance value for the test statistic

Model	$QAIC_c$	*r*	Estimate ± SE	T.S	EDF	*P*
Plant cover	35.8	0.41				
Intercept			–2.44 ± 0.61	–3.96		< 0.01
Trees			1.75 ± 0.45	3.39		< 0.01
Forbs25*				4.07	1.89	0.03
Bare*				6.49	1.92	< 0.01
H′	18.0	0.41				
Intercept			–0.49 ± 0.36	–1.38		0.18
H′				5.19	1.00	0.03

* Variable is square-root transformed

Chaetodipus hispidus. Hispid pocket mice were detected in 13 of 42 trapping grids. Mean capture rate of pocket mice was 0.7 ± 0.2 captures per 100 trapnights, ranging from 0 to 4.4 captures per 100 trapnights. The abundance of pocket mice was explained by a GAM using total grass cover at 50 cm as the explanatory variable, a log link function, and the negative binomial distribution (Table 9). I did not include a random effect in the *C. hispidus* model because there was little variance in capture rate over the sampling season. The final *C. hispidus* model predicted the highest *C. hispidus* abundance between 11% and 20% grass cover at 50 cm (Figure 14). Because *C. hispidus* abundance was always low, I tried modeling its presence or absence but could find no

significant predictors. In other models I found that tree cover, forb cover, and bare ground were not significant predictors of *C. hispidus* abundance or presence.

Table 9. Numerical details of the generalized additive model (GAM) explaining hispid pocket mouse (*Chaetodipus hispidus*) abundance. $QAIC_c$ is Quasi-Akaike Information Criterion for small samples, *r* is Pearson correlation coefficient between fitted values and observed values, estimate is estimate of parametric component, T.S. is the test statistic for each parametric component (*z*) or smoother (χ^2) in GAM, EDF is estimated degrees of freedom used by smoother, and *P* is the significance value for the test statistic

Model	$QAIC_c$	*r*	Estimate ± SE	EDF	T.S.	*P*
Plant cover	15.6	0.47				
Intercept			–0.82 ± 0.31		–2.64	< 0.01
Grass 50				1.86	7.38	0.02

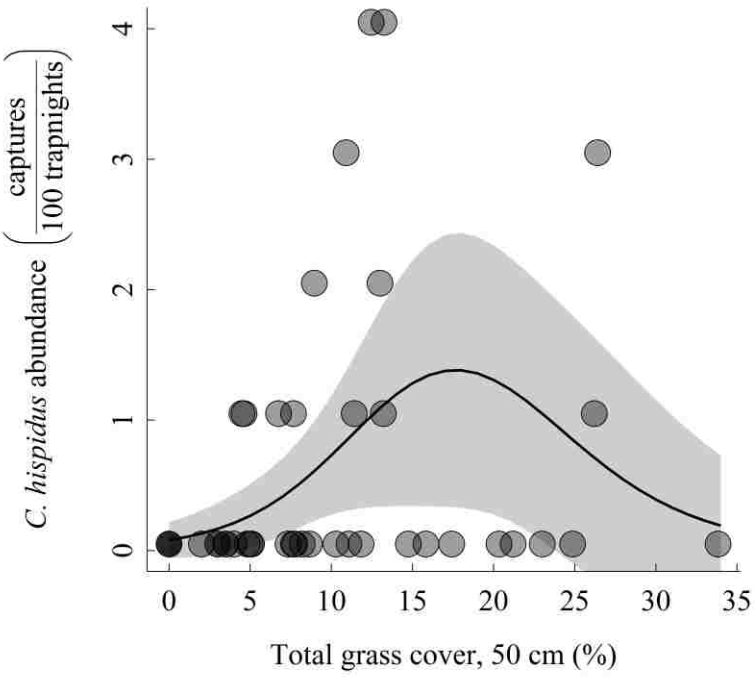

Figure 14. Predictions of a GAM of hispid pocket mouse (*Chaetodipus hispidus*) abundance. Points are observed data; line shows model predictions, and shaded area is the 95% confidence interval

Habitat heterogeneity. Shannon diversity index of plant cover (i.e., plant cover heterogeneity) of sampling grids ranged from 0.13 to 1.44 (mean $H' = 0.68 \pm 0.39$). Heterogeneity was significantly greater in grids with trees present (1.04 ± 0.33) than in grids without trees (0.47 ± 0.26; Kruskal-Wallis $\chi^2 = 20.07$, 1 df, $P < 0.01$). Heterogeneity was positively correlated with bare ground (Pearson's $r = 0.48$, $t = 3.35$, $P < 0.01$) and forb cover (Pearson's $r = 0.62$, $t = 5.06$, $P < 0.01$), and negatively correlated with total grass cover (Pearson's $r = -0.89$, $t = -12.81$, $P < 0.01$). There were weak effects of plant cover heterogeneity on abundance of *S. hispidus* (Table 7) and *P. maniculatus* (Table 8). Generalized additive mixed models predicted that as the plant cover heterogeneity of a sampling grid increased, *S. hispidus* abundance decreased and *P. maniculatus* abundance increased (Figure 15). Plant cover heterogeneity was not a significant predictor of *C. hispidus* abundance.

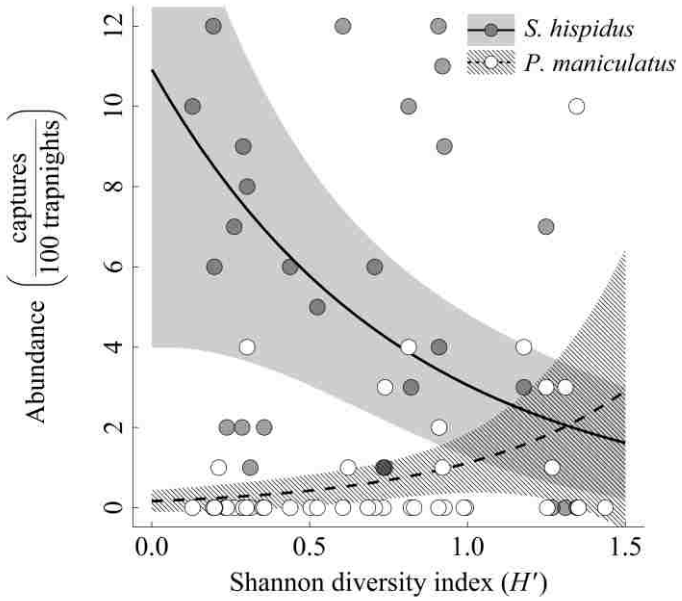

Figure 15. Predictions and 95% CI of generalized additive mixed models of hispid cotton rat (*Sigmodon hispidus*) and deer mouse (*Peromyscus maniculatus*) abundance vs. heterogeneity of plant cover (Shannon diversity index, *H*′)

Discussion

Habitat Associations

Sigmodon hispidus. Grassy ground cover is an important resource for cotton rats both as food and as cover from predators (Cameron and Spencer 1981), and *S. hispidus* is usually associated with tall, thick grass cover (Kaufman and Fleharty 1974; Jones et al. 2003). Goertz (1964) found greater *S. hispidus* abundance when grass cover was deeper and noted that the common denominator of cotton rat habitat was "tall and dense" grass with various forbs and shrubs, independent of plant species composition. The contrast I found between the *S. hispidus* positive response to dominant bluestem and negative response to other grasses (Figure 12b-c) was not expected. Kaufman and Kaufman (1997) reported a positive correlation between cotton rat density and dominant grass stem density in plots but no correlation between cotton rat density and any particular grass species. Relative abundance of non-dominant grasses may be indicative of marginal habitat quality or the legacy of a disturbance before sampling took place.

Because cotton rats spend practically all of their time at ground level, I expected that grass cover close to the ground would best predict *S. hispidus* abundance but instead found that grass cover at greater heights tended to fit the data better. This could result from disturbance and successional history; more grass cover at upper heights should reflect a longer time since disturbance (e.g., fire or grazing) and thus a longer time for *S. hispidus* populations to establish and grow.

All models of *S. hispidus* abundance showed increasing uncertainty in their predictions as grassy ground cover increased (Figure 12a-c). Birney et al. (1976) found a similar pattern in response of meadow voles (*Microtus pennsylvanicus* (Ord 1815)) to

total ground cover. They hypothesized that *M. pennsylvanicus* responses to microhabitat could occur at thresholds rather than continuously. In their data voles avoided habitat below 400 g/m^2 of plant cover, and variation in cover > 600 g/m^2 did not affect vole abundance. Similarly, if *S. hispidus* abundance does not respond to grass cover variance above a certain threshold, then the wide spread of the model predictions could reflect ecological indifference rather than poor model fit.

Non-grass ground cover had weaker effects on cotton rat abundance than did grasses. The presence of trees decreased cotton rat abundance, probably because of reduced grassy ground cover under or near wooded patches on prairie landscapes. Contrary to expectations, non-grass herbaceous vegetation did not significantly affect cotton rat abundance. Cameron and Spencer (2008) found that herbaceous dicots constitute an important part of cotton rat diets during reproductive periods and that cotton rats often select territories to include some forbs.

Modeling *S. hispidus* response to bare ground was problematic. Cotton rats generally avoid bare ground, but my initial model predicted that *S. hispidus* abundance actually increases at high levels (>25%) of bare ground. When I removed 3 trapping grids with similarly high bare ground cover and refit the model, bare ground decreased cotton rat abundance (Figure 12d), a finding more consistent with other studies (Cameron and Spencer 1981; Kaufman and Kaufman 1997). The response to so much bare ground may have actually been a macrohabitat effect (Morris 1984) masking or altering a more typical microhabitat association. Other than the unimportance of forb cover, my findings agree with previous literature on cotton rat habitat use (Kaufman and Fleharty 1974; Cameron and Spencer 1981; Kaufman and Kaufman 1997; Hanchey and Wilkins 1998).

Peromyscus maniculatus. Deer mice were most abundant in sampling grids with trees present and with intermediate values of forb ground cover and bare ground (Figure 13). Grass cover was not a significant predictor of *P. maniculatus* abundance. Grids with more *P. maniculatus* also tended to have greater heterogeneity in plant cover. Avoidance of habitat with extreme values of forb cover indicates that *P. maniculatus* prefers heterogeneous habitats, rather than habitat with an abundance of one particular kind of vegetation. *Peromyscus maniculatus* is often found in structurally complex habitat (Holbrook 1978; Carey and Wilson 2001).

Chaetodipus hispidus. The only significant environmental predictor of pocket mouse abundance was grass cover at 50 cm (Table 9). Pocket mouse abundance was highest at intermediate values of grass cover (Figure 14). Unlike *S. hispidus* (below), *C. hispidus* abundance declined with high grass cover, peaking between 10% and 20% coverage at 50 cm. I tested total grass at other heights but 50 cm gave the best fit to the data. I thought that this might indicate a negative interaction between these 2 species, but there was no significant correlation between their abundances. Thus the unexplained variation in *C. hispidus* abundance apparently is not caused by interspecific interactions with cotton rats. This association of pocket mice with intermediate levels of ground cover was also reported by Jones et al. (2003). Fuhlendorf et al. (2010), Bock et al. (2011), and Kirchner et al. (2011) found *C. hispidus* was most abundant in recently disturbed grasslands, particularly after fires which remove a large proportion of grassy ground cover. I avoided sampling habitats which showed signs of recent fire or other disturbance, but most *C. hispidus* were found where grass cover was moderate. Pocket mice are usually found in habitats with at least one moderately dense forb or shrub

species (Paulson 1988; Schmidly 2004) but I found no association of pocket mice with forb cover. I also found no relationship between *C. hispidus* abundance and habitat heterogeneity.

I found few strong environmental predictors of *C. hispidus* abundance. This may have been caused by a very low capture rate of *C. hispidus*, or a real lack of strong habitat associations. When I fit vectors of small mammal abundances to an ordination (nonmetric multidimensional scaling) of plant cover I noticed that *C. hispidus* abundance was mostly orthogonal to most cover categories. This weak fit between *C. hispidus* abundance and dense cover in both ordinations and additive models further supports the hypothesis that this species prefers intermediate levels of ground cover.

Comparison of Species

Sigmodon hispidus, *P. maniculatus*, and *C. hispidus* responded to habitat in different ways. Grass abundance was an important driver of both *S. hispidus* and *C. hispidus* abundance, but not of *P. maniculatus* abundance. Whereas *S. hispidus* responded monotonically to habitat variables, *C. hispidus* and *P. maniculatus* were most abundant at intermediate values of plant cover. Non-grass plant cover had the greatest effect on deer mice. When significant, presence of trees reduced both *S. hispidus* and *C. hispidus* abundances, and increased *P. maniculatus* abundance. Habitat heterogeneity had a positive effect on *P. maniculatus* abundance, a negative effect on *S. hispidus* abundance (Figure 15), and no effect on *C. hispidus* abundance.

The most abundant species in this study, *S. hispidus*, commonly responds positively to grassy habitat at all scales (Goertz 1964; Cameron and Spencer 1981) regardless of grass identity, meaning it is a specialist of grassy macrohabitats but a

microhabitat generalist within grassland macrohabitat. The negative association between *S. hispidus* and some grass species suggests that grass identity is only important at small spatial scales and is less important than overall grass abundance and structure. Because cotton rats depend on grass both for food and for shelter (Cameron and Spencer 1981) it is unsurprising that they would avoid habitat with diverse vegetation. Fuhlendorf et al. (2010) also found that cotton rats preferred homogeneous habitats. Deer mice, on the other hand, are generalists of macrohabitats and specialists of microhabitats, being present and abundant in a wide variety of ecotypes (Coppeto et al. 2006). I found that deer mice used heterogeneous habitats with moderate to high structural complexity. *Chaetodipus hispidus* is found in a wide variety of grassland vegetation and soil types over its range (Paulson 1988) but its abundance at small scales seems to be driven by disturbance and structural complexity of habitat. This means it is a generalist of macrohabitats but a specialist of disturbed or complex microhabitats with friable soils. The differing responses to bare ground and plant cover may be caused by alteration of microhabitat response by macrohabitat type (Jorgensen and Demarais 1999b). Small mammals select habitat at multiple spatial scales (Morris 1984; Orrock et al. 2000) with responses to microhabitat variables (e.g., plant cover) constrained by macrohabitat type (e.g., arroyos vs. uplands, or forests vs. grasslands; Jorgensen and Demarais 1999b). I sampled only one macrohabitat type (little bluestem-indiangrass mixed prairie) at a small scale (tens of meters), so cannot draw direct conclusions about macrohabitat selection.

Biogeographic Considerations

I captured 5 species of grassland-occurring rodents at LBJNG. Based on distributional maps and known county records (Dalquest and Horner 1984; Schmidly

2004) I expected but did not find Texas mouse (*Peromyscus attwateri* J. A. Allen 1895), white-ankled mouse (*Peromyscus pectoralis* Osgood 1894), western harvest mouse (*Reithrodontomys montanus* (Baird 1855), or *Baiomys taylori*. Several rodent species characteristic of wooded habitat known to occur in Wise County or an adjacent county include *Neotoma floridana*, southern plains woodrat (*Neotoma micropus* Baird 1855), and *Microtus pinetorum*. I probably did not detect these species because I trapped near the boundaries of wooded patches but not in them. I did not survey fossorial mammals or insectivorans but Pitts et al. (2001) found *Cryptotis parva*, eastern mole (*Scalopus aquaticus* (Linneaus 1758)), and plains pocket gopher (*Geomys bursarius* (Shaw 1800)) at or near LBJNG in 1999. I observed but did not capture fox squirrel (*Sciurus niger* Linneaus 1758), swamp rabbit (*Sylvilagus aquaticus* (Bachman 1837)), eastern cottontail (*Sylvilagus floridanus* (J. A. Allen 1890), striped skunk (*Mephitis mephitis* (Schreber 1776)), raccoon (*Procyon lotor* (Linneaus 1758)), Virginia opossum (*Didelphis virginianus* Kerr 1792), white-tailed deer (*Odocoileus virginianus* (Zimmerman 1780)), and nine-banded armadillo (*Dasypus novemcinctus* Linneaus 1758). Another small mammal survey in the Grand Prairie in Johnson County, Texas (approximately 125 km to the south of LBJNG) found *P. attwateri*, *P. maniculatus*, *P. pectoralis*, *B. taylori*, *R. fulvescens*, *S. hispidus*, and *N. micropus* (Hanchey and Wilkins 1998). The habitat associations they report for *P. maniculatus* and *S. hispidus* are similar to those in the present study.

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CHAPTER FOUR

Organismal and Environmental Drivers of Serum Leptin Concentration in *Sigmodon hispidus*

Abstract

Leptin, a hormone secreted by adipose tissue, is a critical regulator of energy and lipid metabolism in mammals. Serum leptin concentration (SLC) is proportional to energy availability and overall adiposity in many species. I investigated what organismal and environmental characteristics drive SLC in the hispid cotton rat, *Sigmodon hispidus* (Say and Ord 1825). I also investigated whether body mass, a potential driver of SLC, was correlated with habitat quality. I found that males were more massive than nonpregnant females and that reproductive individuals were significantly more massive in both sexes. The distribution of body mass varied with plant cover, shifting downward with increased grass cover and upward with increasing dicot forbs cover. Drivers of SLC were less clear. Overall, SLC was limited by body mass and dicot forbs cover and decreased slightly with increasing bare ground. When sexes were analyzed separately, male SLC was limited by availability of any type of food (grasses or dicot forbs) while lower limit of female SLC decreased with increasing grass cover. I conclude that simple caloric abundance is not an adequate predictor of body mass or satiety; that the sexual dimorphism in the SLC-environment relationship was caused by differing nutritional demands of reproduction; and that SLC has promise as a non-invasive marker of energy availability but that more study is needed. To my knowledge this is the first examination of leptin in *S. hispidus*.

Introduction

The hispid cotton rat (*Sigmodon hispidus* Say and Ord 1825) is an herbivorous small mammal common throughout the southeastern United States and parts of northern Mexico. *Sigmodon hispidus* exploits a variety of food sources, including grasses, seeds, berries, and insects (Cameron and Spencer 1981) but its primary food source is grasses (Goertz 1964; Fleharty and Olson 1969). Grasses are foods rich in carbohydrates and indigestible cellulose, but largely deficient in proteins and lipids; this deficiency is especially pronounced in grasses utilizing the C_4 photosynthetic pathway (Barbehenn et al. 2004). Grasses also form the structure of *S. hispidus* habitat, providing cover and nesting material.

Many prairie habitats hosting *S. hispidus* also include dicotyledonous forbs, which are less abundant than grasses but have a lower C:N ratio and are richer in amino acids, lipids, and other nutrients (Kincaid and Cameron 1985; Randolph et al. 1991; Cameron and Eshelman 1996; Schetter et al. 1998). Randolph and Cameron (2001) found that cotton rats can maximize energy gain (and minimize time costs) by foraging in monocot-only habitat, but at the cost of dietary deficiencies of amino acids, P, and Ca during reproduction. The additional energetic and elemental requirements of pregnancy and lactation explain why reproductive females are commonly associated with a mixed monocot-dicot habitat (Kincaid and Cameron 1985; McMurry et al. 1994; Cameron and Spencer 2008). Spatial association with mixed habitats allows for both sufficient intake of calories (from monocots) and sufficient intake of proteins and minerals (from dicots). Laboratory trials have also shown that *S. hispidus* will select a variety of food items to form a complete diet (Harriman 1977).

Kincaid and Cameron (1985) found that cotton rats rarely eat only grasses, even though grasses constitute ≥ 90% of the available plant mass in their habitat, and that they will expend extra search effort to include both grasses and forbs in their diet. Cotton rats get most of their nutrition from grasses, but dicot forbs can be important supplemental sources of nutrition for reproductive females (Randolph et al. 1991, 1995; Randolph and Cameron 2001; Cameron and Spencer 2008). The benefits of such supplementation decrease with body mass and smaller cotton rats in general are most sensitive to habitat quality (Slade et al. 1996). This may explain why Mattingly and McClure (1985) found that impact of food deprivation on neonatal survival decreases with increasing maternal mass. Doonan and Slade (1995) found that smaller *S. hispidus* were most likely to emigrate to food-supplemented patches, whereas Sulok et al. (2004) found no relationship between mass class and response to food supplementation. McMurry et al. (1994) found that mass-specific litter sizes were greatest in monocot dominated habitats, while Slade et al. (1996) found no such relationship. In aggregate, these studies suggest that habitat associations in *S. hispidus* can vary with age, reproductive status, and sex in accordance with individuals' current needs.

Cameron et al. (2009) measured fiber, lipid, protein, and soluble carbohydrates in several classes of coastal prairie plant, and found that dicots offered more nutrition and less fiber than sympatric monocot grasses. However, such dicot forbs are not good predictors of *S. hispidus* abundance (Chapter 3). Cotton rat density is positively associated with grass cover (Goertz 1964), and grass cover also seems to enhance mass-specific growth and reproductive rates (Slade et al. 1996). Randolph and Cameron (2001) found that this was because standing crops of energy and total nutrients were

larger in monocot patches compared to dicot or mixed patches, and exhibited less seasonal variability. The stability and abundance of monocots as a food resource for nonreproductive individuals contributes to their importance.

Serum Leptin Concentration: Drivers and Roles

Leptin is a peptide hormone encoded by the *Ob* gene and produced primarily by adipose tissue (Reidy and Weber 2000). In mammals, leptin regulates appetite and lipid reserves (Reidy and Weber 2000), puberty and reproduction (Cunningham et al. 1999; Margetic et al. 2002), and body temperature (Henry et al. 2011). Circulating levels of leptin in the blood are strongly tied to a mammal's energy balance, and several studies have found that leptin helps mediate energy metabolism independent of food intake (Elmquist 2001; Rayner and Trayhurn 2001; Margetic et al. 2002). Laboratory studies have shown a strong relationship between SLC and body mass index, fat mass, or energy balance in humans and most rodents (Maffei et al.1995) but not in carnivores, shrews, bats, and hamsters (Niemenen 2000; Schneider et al. 2000). Serum leptin concentration has been found to be positively correlated with body fat percentage (Hamilton et al. 1995; Maffei et al. 1995; Klein et al. 1996; Landt et al. 1998) and food intake regardless of body fat (Ahima et al. 1996; Ahren et al. 1997; Dubuc et al. 1998; Reidy and Weber 2000). Landt et al. (1998) found that SLC increased more quickly with body fat percentage in males than in female *Rattus*; this dimorphism is reversed in humans (Saad et al. 1997). In *Mus*, Frederich et al. (1995) found that the magnitude of SLC response to body fat was similar between the sexes. Extrinsic mechanisms such as temperature and photoperiod can also affect SLC and leptin sensitivity (Król et al. 2006; Li and Wang 2007).

Previous studies of leptin in wild mammals have investigated its role in thermogenesis, reproduction, and seasonal behavior. Yang et al. (2011) found that leptin in plateau pika (*Ochotona curzoniae* (Hodgson 1858)) was crucial for adaptive thermogenesis. In wild rodents, numerous studies have found that leptin helps regulate seasonal fluctuations in body mass (Li and Wang 2007; Zhang and Wang 2007) and/or adaptive thermogenesis (Wang et al. 2006; Li and Wang 2007; Zhang and Wang 2007). Leptin resistance can arise in animals when energy intake should not be inhibited. For example, Zhang and Wang (2008) found that hypothalamic resistance to leptin in Brandt's voles (*Lasiopodomys brandtii* (Radde 1861)) acted to stimulate energy intake during lactation and pregnancy. In a controlled experiment, Gutman et al. (2008) found that exogenous leptin could not overcome the drive to eat in food-deprived golden spiny mice (*Acomys russatus* (Wagner 1840)). Seasonal leptin resistance is mediated by photoperiod (Rousseau et al. 2002). Niemenen (2000) suggested that endogenous cycles of leptin secretion in animals with strongly seasonal life histories might overwhelm the regulation of SLC by energy balance and cautioned (based on studies in mink) that the role and regulation of leptin can vary with body size and sex. Decoupling of SLC from body composition seems to be caused by seasonal variation in hypothalamic leptin receptors, whereby less active forms of the receptor predominate during times when the body needs to put on fat (i.e., when the hunger-suppressing side of the leptin cycle must be inhibited). Studies conducted over shorter time spans (< 1 season) should still be able to assume that energy balance and SLC are connected.

Because SLC is driven by both body composition (Reidy and Weber 2000) and by short-term satiety (Nieminen 2000), it might be suitable for use as a non-invasive direct

indicator of body condition and an indirect indicator of forage quality within a habitat. Such an indicator would be useful because it would enable ecologists to estimate how successfully an animal has been foraging and to compare relative foraging success between habitats, without sacrificing large numbers of animals (Chapter 1). Numerous morphological and chemical indicators of nutritional status have been suggested (Stevenson and Woods 2006; Homyack 2010) which all assume a mechanistic link between habitat quality and some measurable parameter. I measured SLC in *S. hispidus* in relation to habitat quality as a test of its suitability as a body condition indicator.

Questions and Hypotheses

My objective was to investigate what organismal and environmental factors might influence body mass and serum leptin concentration (SLC) in *S. hispidus*. I hypothesized that: 1) Mass and SLC are greater in males than nonpregnant females; 2) SLC varies with reproductive condition in females but not in males; 3) Body mass and SLC covary positively; 4) Mass is positively associated with grass cover, and negatively associated with bare ground and non-grass cover; 5) SLC is positively associated with grass cover, and negatively associated with bare ground and non-grass ground cover; 6) Habitat characteristics drive SLC differently in females and males; and 7) SLC is negatively associated with abundance because of intraspecific competition.

Methods and Materials

Sample Collection

Field sampling methods were described in Chapter 3. Small mammals were sampled in 14 weekly trapping sessions from 3 May to 4 August 2011 at the Lyndon B.

Johnson National Grasslands (LBJNG) near Decatur, Wise County, Texas (Figure 11). The LBJNG is an 8218 ha network of 67 managed units mostly within the Cross Timbers Level III ecoregion (Wilken et al. 2011). In each trapping session I set 3 grids of 30 Sherman traps (8 × 9 × 23 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida, USA) for 3 consecutive nights. Traps were checked each morning, left closed during the day, and collected after the 3rd morning. Each trap was baited with 5 g of crimped oats.

All procedures involving live animals were approved by the Baylor University Animal Care and Use Committee and were in accordance with the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011). Sampling was carried out under a Texas Parks and Wildlife Scientific Collection Permit and a United States Forest Service Special Use Permit.

I also sampled plant cover using a modification of the canopy-cover method of Daubenmire (1959) at 6 to 12 trap stations per grid. Within a 0.1 m^2 quadrat at each station I visually estimated the percentage of ground covered by grass, dicot forbs, and bare ground as being in 1 of 6 ranges: 0%, 1% to 5%, 6% to 25%, 26% to 50%, 51% to 75%, 76% to 95%, and 96% to 100%. The percentage of cover in a category was analyzed as the midpoint of that range. I also recorded presence or absence of trees as a binary factor (Chapter 3).

Quantifying Serum Leptin Concentration

I took a blood sample of 50 to 300 μL from the saphenous veins of cotton rats weighing ≥ 30 g. Only one sample was taken from each individual. To sample blood I shaved a hindlimb, swabbed the skin with a disposable isopropanol pad to reduce the probability of infection, and punctured the saphenous vein with a new sterile 21 or 23

gauge hypodermic needle. Blood was collected with a 300 μL capillary blood collection tube (Microvette™ 300 Serum, Sarstedt AG & Co., Nümbrecht, Germany). Blood samples were centrifuged at 2000 × *g* for 15 min and serum was pipetted off and stored in a clean microcentrifuge tube. Samples collected on the first 2 mornings of a session were stored at 0 °C near the field site; on the last morning of each session I returned to the laboratory and stored all blood samples at –80 °C until analysis. Samples were kept at or below 0 °C during transit.

I quantified SLC in all samples using enzyme-linked immunosorbent assay (ELISA) for rat leptin (catalog #KEC2281, lot 955384A, Invitrogen Corporation, Camarillo, California, USA) on 16 December 2011. Sample absorbencies were read on a Biotek ELx800 plate reader. A standard curve (3 parameter logistic) was generated with samples of known concentrations of 0, 62.5, 125, 250, 500, 1000, 2000, and 4000 pg/mL purified *E. coli*-expressed recombinant Rt leptin. The standard curve model was backsolved for each sample and the resulting value multiplied by 5 to account for pre-assay dilution. The mean of 2 duplicates for was used for all standards and for most samples (some samples were large enough for only one assay). Detectable range of leptin using these kits was 250 to 16×10^3 pg/ml.

Data Analysis

I used a three parameter logistic model to relate absorbance readings to standard Rt leptin concentrations, then used this model to predict unknown leptin concentrations from absorbance of samples. Because of non-normality and leptokurtosis in SLC, I used Wilcoxon rank-sum tests to check for differences in SLC between classes of animals (e.g., males vs. females). I used quantile regression to model the distributions of SLC

and mass using organismal and environmental variables as predictors. Quantile regression estimates rates of change (slopes) for conditional quantiles of the response variable rather than a single slope for the mean of a response distribution (Cade and Noon 2003). This allows analysis of rates of change in heterogeneous distributions that might be missed by linear models, such as ecological limitation (Cade et al. 1999). I fit models for the 10th, 30th, 50th, 70th, and 90th percentiles of each response variable. These quantiles were chosen to represent a wide range of each response variable, including central tendency (50th percentile), lower and upper envelopes (10th and 90th percentiles), and lower and upper thirds (30th and 70th percentiles). I used linear models to check for a temporal trend in mass and SLC, and Mantel tests to check for spatial and temporal autocorrelation in mass and SLC data. All analyses were performed in R version 2.13.1 (R Development Core Team 2011). I used package drc version 2.2–1 (Ritz and Streibig 2005) for determining SLC from absorbency data and package quantreg version 4.76 (Koenker 2011) for quantile regressions.

Results

Animal Mass Data

Summary of mass data is shown in Table 10. Among all animals, mean mass did not differ between the sexes ($W = 1134.5$, $P = 0.19$). Males were more massive than nonpregnant females ($W = 880.5$, $P = 0.04$). Within each sex, mass varied with reproductive condition. Pregnant females were significantly heavier than nonpregnant females ($W = 8.5$, $P < 0.01$). Scrotal males were heavier than nonscrotal males ($W = 418.5$, $P = 0.02$). Juvenile animals were significantly smaller than adult animals in

females ($W = 72$, $P < 0.01$), males ($W = 164.5$, $P < 0.01$), and when all animals were combined ($W = 880.5$, $P = 0.04$).

Table 10. Summary of masses (g) of hispid cotton rats (*Sigmodon hispidus*) captured at the Lyndon B. Johnson National Grasslands. Values reported are $\bar{x} \pm$ SE with sample size below in parentheses

Grouping	All animals[a]	Females[b]	Males
All animals	101.3 ± 4.6 (n = 93)	92.8 ± 7.8 (n = 33)	106.1 ± 5.9 (n = 59)
Adults	106.5 ± 4.4 (n = 87)	99.4 ± 7.6 (n = 30)	110.3 ± 5.4 (n = 56)
Juveniles	26.0 ± 2.0 (n = 6)	26.7 ± 3.2 (n = 3)	25.3 ± 3.2 (n = 3)
Reproductive		150.2 ± 10.5 (n = 6)	118.4 ± 5.7 (n = 42)
Nonreproductive		85.1 ± 7.1 (n = 23)	86.1 ± 11.2 (n = 14)

[a]One adult individual is included only in the "all animals" column because sex was not recorded

[b]One female was omitted from the "reproductive" and "nonreproductive" groups because reproductive status was indeterminate

Among all animals the mass distribution shifted downward with increasing grass cover, and shifted upward with increasing bare ground and forbs cover (Table 11, Figure 16). Only the grass and forbs cover patterns were significant among females (Table 12); among males all three patterns were significant (Table 13). Fourteen sampling grids had some tree cover, but total overhead canopy cover never exceeded 15%. Mean animal mass did not differ between grids with trees present (112.8 ± 8.6 g, n = 28) and grids with no trees present (96.4 ± 5.3 g, n = 65; $W = 696.5$, $P = 0.07$). Among females, mean mass

did not differ between grids with trees (106.4 ± 13.7 g; $n = 12$) and grids without trees (85.1 ± 9.2 g, $n = 21$; $W = 92$, $P = 0.21$). Among males, mean mass did not differ between grids with trees (118.4 ± 11.9 g, $n = 15$) and grids without trees (101.8 ± 6.4 g, $n = 44$; $W = 260$, $P = 0.23$).

Table 11. Numerical details of quantile regression models relating body mass of hispid cotton rats (*Sigmodon hispidus*) to plant cover. The column τ denotes the response quantile (e.g., τ = 0.3 signifies 30th percentile). Nonsignificant models are not shown

τ	Parameter	Estimate ± SE	*t*	*P*
0.3	Intercept	146.29 ± 36.49	4.01	< 0.01
	Grass cover, 10 cm (%)	–0.96 ± 0.49	–1.93	0.06
0.5	Intercept	149.01 ± 18.81	7.92	< 0.01
	Grass cover, 10 cm (%)	–0.63 ± 0.28	–2.25	0.03
0.9	Intercept	219.95 ± 26.67	8.25	< 0.01
	Grass cover, 10 cm (%)	–0.84 ± 0.35	–2.40	0.02
0.3	Intercept	8.96 ± 2.63	3.40	< 0.01
	Bare ground (%)[a]	18.54 ± 27.26	0.68	< 0.01
0.3	Intercept	18.54 ± 27.26	0.68	0.50
	Forbs cover, 10 cm (%)[a]	16.22 ± 7.87	2.06	0.04
0.5	Intercept	58.49 ± 13.85	4.22	< 0.01
	Forbs cover, 10 cm (%)[a]	12.67 ± 3.26	3.89	< 0.01
0.7	Intercept	74.30 ± 18.82	3.95	< 0.01
	Forbs cover, 10 cm (%)[a]	13.24 ± 4.98	2.66	< 0.01
0.9	Intercept	109.75 ± 16.96	6.47	< 0.01
	Forbs cover, 10 cm (%)[a]	11.68 ± 3.70	3.15	< 0.01

[a]Variable is square-root transformed

Table 12. Numerical details of quantile regression models relating body mass of female hispid cotton rats (*Sigmodon hispidus*) to habitat characteristics. The column τ denotes the response quantile modeled (e.g., τ = 0.3 signifies 30th percentile)

τ	Parameter	Estimate ± SE	*t*	*P*
0.1	Intercept	62.92 ± 9.81	6.41	< 0.01
	Grass cover, 50 cm (%)	–1.69 ± 0.68	–2.49	0.02
0.9	Intercept	94.67 ± 26.47	3.57	< 0.01
	Forb cover, 10 cm (%)[a]	13.93 ± 7.14	1.95	0.06

[a]Variable is square-root transformed

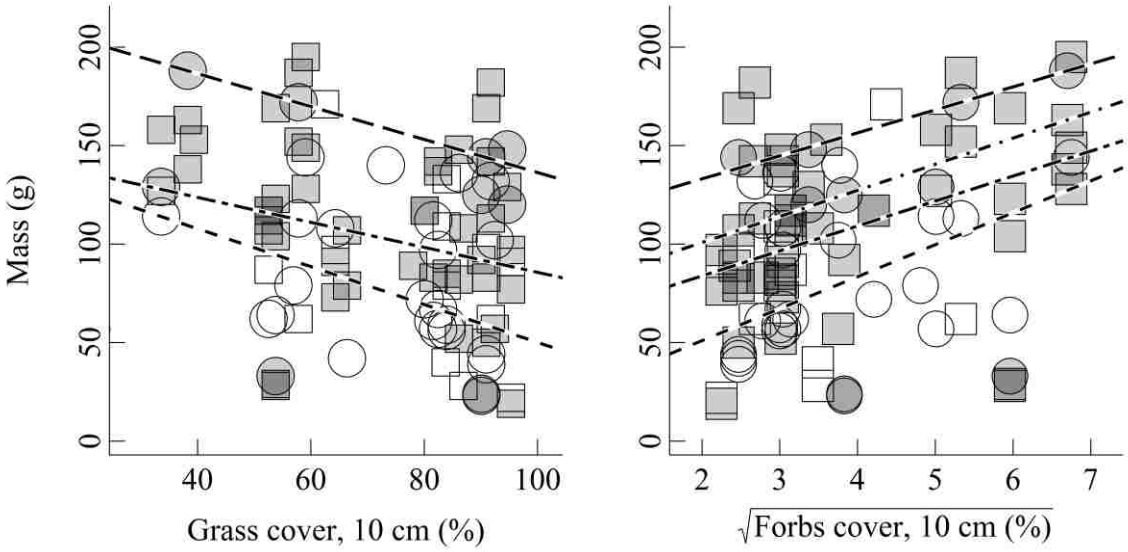

Figure 16. Quantile regressions of hispid cotton rat (*Sigmodon hispidus*) body mass vs. plant cover. Circles represent females and squares represent males; shaded symbols are animals captured in reproductive condition. In the grass cover plot the lines represent 30th, 50th, and 90th percentiles; in the forbs cover plot the quantiles shown are the 30th, 50th, 70th, and 90th percentiles

Table 13. Numerical details of quantile regression models relating body mass of male cotton rats (*Sigmodon hispidus*) to plant cover. Column τ denotes the response quantile modeled (e.g., τ = 0.3 signifies 30th percentile). Nonsignificant models are not shown. Environmental correlates of SLC in males are similar to those for all animals (Table 11)

τ	Parameter	Estimate ± SE	*t*	*P*
0.1	Intercept	166.81 ± 66.57	2.51	0.02
	Grass cover, 10 cm, (%)	–1.52 ± 0.79	–1.91	0.06
0.3	Intercept	159.76 ± 24.09	6.63	< 0.01
	Grass cover, 10 cm, (%)	–0.98 ± 0.36	–2.70	< 0.01
0.5	Intercept	154.96 ± 20.08	7.72	< 0.01
	Grass cover, 10 cm, (%)	–0.72 ± 0.27	–2.64	0.01
0.7	Intercept	187.83 ± 22.26	8.44	< 0.01
	Grass cover, 10 cm, (%)	–0.88 ± 0.33	–2.66	0.01
0.1	Intercept	32.25 ± 14.72	2.19	0.03
	Bare ground, (%)*	10.90 ± 4.04	2.70	< 0.01
0.3	Intercept	75.71 ± 10.07	7.52	< 0.01
	Bare ground, (%)*	7.23 ± 3.00	2.41	0.02
0.5	Intercept	62.00 ± 18.94	3.53	< 0.01
	Forbs cover, 10 cm, (%)*	12.89 ± 4.11	3.14	< 0.01
0.7	Intercept	66.82 ± 18.94	3.53	< 0.01
	Forbs cover, 10 cm, (%)*	15.98 ± 4.81	3.32	< 0.01
0.9	Intercept	107.10 ± 30.13	3.55	< 0.01
	Forbs cover, 10 cm, (%)*	13.02 ± 6.54	1.99	0.05

* Variable is square-root transformed

Serum Leptin Concentration Data

I took samples from 107 cotton rats; 93 of these samples (59 male, 33 female, 1 unrecorded sex) were large enough to assay. Summary SLC data for all individuals are shown in Table 14. Mean SLC did not vary between males and females ($W = 845.5$, $P = 0.29$). Mean SLC also did not vary between juvenile and adult animals ($W = 246.5$, $P = 0.86$); nor did it vary between juvenile and adult females ($W = 43$, $P = 0.93$) nor juvenile and adult males ($W = 82$, $P = 0.96$). Among adult females, SLC did not differ between pregnant and nonpregnant animals ($W = 74$, $P = 0.81$). Among adult males, SLC did not differ between scrotal and nonscrotal animals ($W = 283$, $P = 0.84$). I detected no linear pattern in mean SLC or variance in SLC over time and found no autocorrelation due to time (Mantel's $r = –0.06$, $P = 0.92$).

Table 14. Summary of serum leptin concentrations (pg/ml) of hispid cotton rats (*Sigmodon hispidus*) captured at the Lyndon B. Johnson National Grasslands during summer 2011. Values reported are $\bar{x} \pm$ SE. Sample sizes are the same as in Table 10

Group	All animals	Females	Males
All animals	1021 ± 22.9	1050 ± 43.5	1005 ± 26.1
Adults	1021 ± 24.3	1055 ± 47.3	1003 ± 27.5
Juveniles	1015 ± 40.0	997 ± 87.1	1034 ± 7.4
Reproductive		1002 ± 80.4	1012 ± 34.6
Nonreproductive		1069 ± 58.5	978 ± 36.7

Distribution of SLC was limited by body mass in both sexes (Table 15, Figure 17). In females, this pattern was weakly significant and in males there was also a significant decline in the 30th percentile of SLC as mass increased (Table 15). No

quantile of the SLC distribution responded to abundance within a sampling grid (Table 16) in any sex (Table 17, Table 18).

Table 15. Details of quantile regression models relating serum leptin concentration (SLC; pg/ml) to mass (g) in hispid cotton rats (*Sigmodon hispidus*). Column τ denotes the response quantile modeled (e.g., τ = 0.9 signifies 90th percentile)

Data	τ	Explanatory variable	Estimate ± SE	*t*	*P*
All animals	0.9	Intercept	1036.30 ± 57.25	18.10	< 0.01
		Body mass	1.85 ± 0.90	2.04	0.04
Females	0.9	Intercept	965.14 ± 176.26	5.48	< 0.01
		Body mass	5.47 ± 3.12	1.76	0.09
Males	0.3	Intercept	1076.78 ± 69.19	15.56	< 0.01
		Body mass	–1.92 ± 0.92	–2.09	0.04
	0.9	Intercept	1004.53 ± 40.29	24.93	< 0.01
		Body mass	2.02 ± 0.92	2.19	0.03

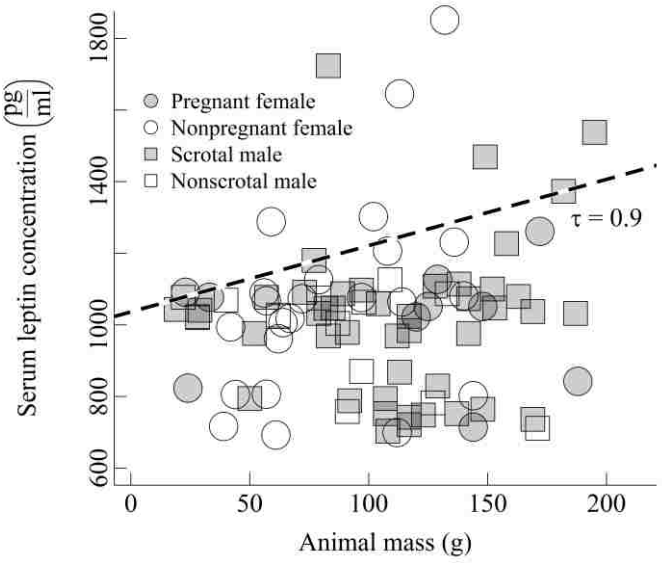

Figure 17. Quantile regression of serum leptin concentration (SLC) vs. body mass of hispid cotton rats (*Sigmodon hispidus*)

Table 16. Details of quantile regressions of serum leptin concentration (SLC; pg/ml) vs. relative abundance (captures per 100 trapnights) of cotton rats (*Sigmodon hispidus*). τ denotes the response quantile (e.g., τ = 0.1 signifies 10th percentile)

τ	Parameter	Estimate ± SE	*t*	*P*
0.1	Intercept	735.99 ± 47.36	15.53	< 0.01
	Abundance	0.90 ± 3.61	0.25	0.80
0.3	Intercept	812.15 ± 113.83	7.13	< 0.01
	Abundance	6.72 ± 5.67	1.18	0.24
0.5	Intercept	1,050.82 ± 27.91	37.64	< 0.01
	Abundance	–1.15 ± 1.91	–0.60	0.54
0.7	Intercept	1,079.88 ± 16.78	64.36	< 0.01
	Abundance	–0.20 ± 1.08	–0.18	0.85
0.9	Intercept	1,301.98 ± 140.45	9.26	< 0.01
	Abundance	–7.20 ± 12.15	–0.59	0.55

Table 17. Details of quantile regressions of serum leptin concentration (SLC; pg/ml) vs. relative abundance (captures per 100 trapnights) in female cotton rats (*Sigmodon hispidus*). τ denotes the response quantile (e.g., τ = 0.1 signifies 10th percentile)

τ	Parameter	Estimate ± *SE*	*t*	*P*
0.1	Intercept	826.74 ± 113.94	7.25	< 0.01
	Abundance	–6.23 ± 8.13	–0.76	0.45
0.3	Intercept	1,004.32 ± 126.37	7.94	< 0.01
	Abundance	–1.86 ± 8.54	–0.22	0.82
0.5	Intercept	1,062.76 ± 46.03	23.08	< 0.01
	Abundance	0.16 ± 3.29	0.04	0.96
0.7	Intercept	1,144.75 ± 86.16	13.28	< 0.01
	Abundance	–2.28 ± 5.19	–0.44	0.66
0.9	Intercept	1,303.39 ± 323.52	4.02	< 0.01
	Abundance	–0.63 ± 20.55	–0.03	0.97

Table 18. Details of quantile regressions of serum leptin concentration (SLC; pg/ml) vs. relative abundance (captures per 100 trapnights) in male hispid cotton rats (*Sigmodon hispidus*). τ denotes the response quantile (e.g., τ = 0.1 signifies 10th percentile)

τ	Parameter	Estimate ± *SE*	*t*	P
0.1	Intercept	706.85 ± 36.56	19.33	< 0.01
	Abundance	3.73 ± 3.92	0.95	0.34
0.3	Intercept	772.94 ± 143.87	5.37	< 0.01
	Abundance	8.40 ± 7.43	1.12	0.26
0.5	Intercept	1038.00 ± 53.54	19.38	< 0.01
	Abundance	–0.60 ± 2.96	–0.20	0.84
0.7	Intercept	1077.99 ± 22.85	47.16	< 0.01
	Abundance	–0.45 ± 1.61	–0.27	0.78
0.9	Intercept	1244.79 ± 172.95	7.19	< 0.01
	Abundance	–4.86 ± 18.09	–0.28	0.78

The distribution of SLC was related to plant cover in both sexes. When all animals were pooled, the 90th percentile increased with forbs cover while the median decreased slightly as bare ground decreased (Table 19, Figure 18).

In females, the 30th percentile of the SLC distribution decreased with increasing grass cover (Table 19, Figure 19). In males, the 90th percentile of SLC increased with grass cover at 50 cm and with forbs cover (Table 19, Figure 19). There was no significant difference in mean SLC among all animals between grids without trees (1006 ± 26.5 pg/ml) and grids with trees (1053 ± 43.2 pg/ml; $W = 787.5$, $P = 0.31$). In females, SLC did not differ between grids with trees (1079 ± 67.1 pg/ml) and grids without trees (1033 ± 57.6 pg/ml; $W = 110$, $P = 0.56$). In males, SLC did not differ between grids with

trees (1037 ± 61.7 pg/ml) and grids without trees (994 ± 28.2 pg/ml; $W = 299.5$, $P = 0.60$).

Table 19. Numerical details of quantile regression models relating serum leptin concentration (pg/ml) to plant cover in hispid cotton rats (*Sigmodon hispidus*). The column τ denotes the response quantile modeled (e.g., τ = 0.9 signifies 90th percentile)

Data	τ	Explanatory variable	Estimate ± SE	*t*	*P*
All animals	0.9	Intercept	1073.00 ± 11.67	91.94	< 0.01
		Forbs cover, 50 cm (%)[a]	93.83 ± 53.04	1.77	0.08
	0.5	Intercept	1058.99 ± 15/63	67.75	< 0.01
		Bare ground (%)[a]	–14.94 ± 8.75	–1.71	0.09
Females	0.3	Intercept	1053.85 ± 79.88	13.18	< 0.01
		Grass cover, 50 cm (%)	- 9.96 ± 5.32	–1.87	0.07
Males	0.9	Intercept	939.65 ± 106.51	8.82	< 0.01
		Grass cover, 50 cm (%)	23.18 ± 10.71	2.17	0.03
	0.9	Intercept	881.00 ± 176.85	4.98	< 0.01
		Forbs cover, 10 cm (%)[a]	87.11 ± 46.79	1.86	0.06

[a]Variable was square-root transformed.

Discussion

Predictions 1 and 2: Organismal Drivers of Mass and Serum Leptin Concentration

Body mass results (males larger than nonpregnant females, pregnant females the most massive, and juveniles of both sexes the least massive) concur with previous work (Chipman 1965). The finding that scrotal males were larger than nonscrotal adult males was unexpected, given that mass alone is a poor predictor of reproductive condition in male *S. hispidus* (McCravy and Rose 1992). Larger animals have a smaller surface area-

to-volume ratio than smaller animals, so in hot weather larger males are more likely to make their testes scrotal for thermoregulation (mean daily low temperature during the study period was 21.0 ± 5.8 °C; mean daily high temperature was 33.6 ± 5.5 °C). Thus the scrotal condition may be an effect of mass, not a cause.

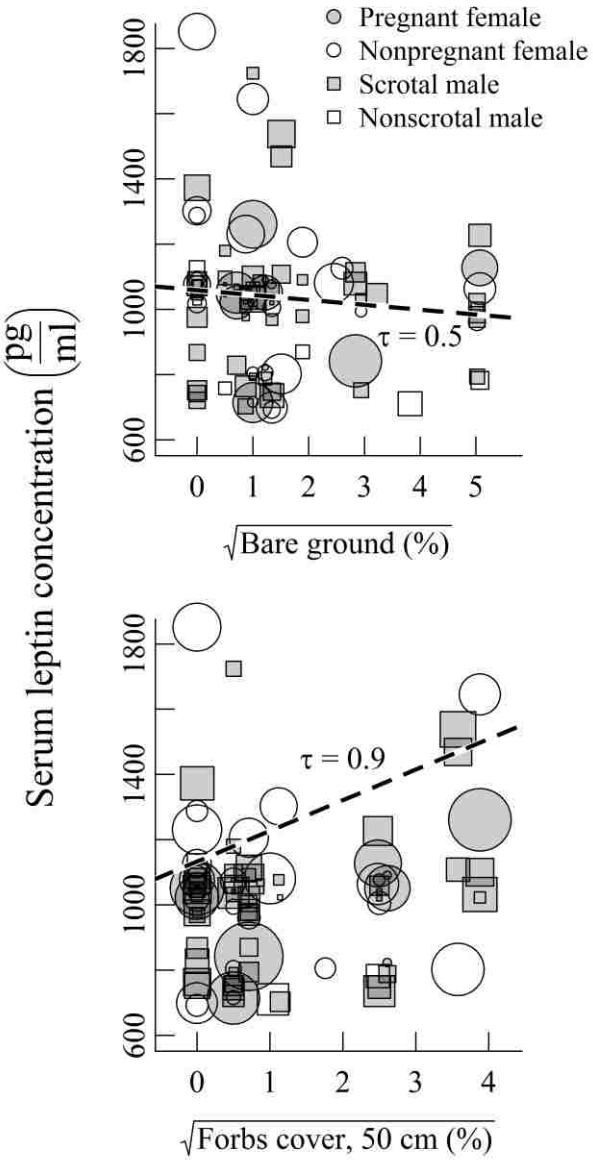

Figure 18. Quantile regressions of serum leptin concentration (SLC) in hispid cotton rats (*Sigmodon hispidus*) vs. plant cover. Points are scaled by animal mass. τ is quantile modeled; e.g., τ = 0.9 signifies 90th percentile

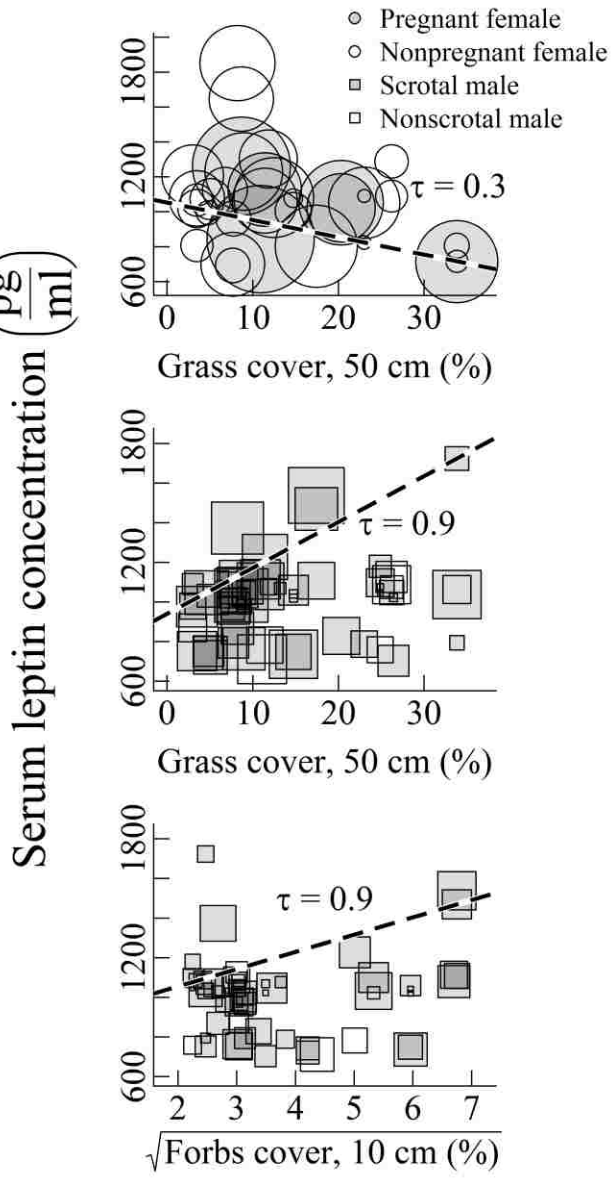

Figure 19. Serum leptin concentration (SLC) responded differently to plant cover in male and female hispid cotton rats (*Sigmodon hispidus*). Points are scaled by animal mass. τ is response quantile: $\tau = 0.3$ signifies 30th percentile, $\tau = 0.9$ signifies 90th percentile

Serum leptin concentration did not vary with any organismal characteristic other than mass. Sexual dimorphism in SLC has been reported in other rodents (Landt et al. 1998) and in humans (Saad et al. 1997), with the more adipose sex having higher SLC. The lack of such a difference in this study could have been caused by the time of year: overall lipid and energy content in *S. hispidus* is lowest during spring and summer (Fleharty et al. 1973; Cameron et al. 1979), so SLC in this population may have been too low to allow sex-based differences. Longer day lengths in summer may also have affected SLC values because of the effect of inhibitory effect of melatonin on leptin secretion in rodents (Ambid et al. 1998; Canpolat et al. 2001; Nieminen et al. 2002).

The lack of a relationship between SLC and reproductive condition in males was not surprising. Males make their testes scrotal for testicular thermoregulation and for reproduction (McCravy and Rose 1992). Although leptin affects thermoregulation by promoting thermogenesis (Dulloo et al. 2002; Zhang and Wang 2007), there was little need for excess thermogenesis during the warm temperatures throughout the study period. Leptin affects reproduction in small mammals (Caprio et al. 2001; Zieba et al. 2005), acting as a signal to permit reproduction when energy intake is sufficient. However, whether or not leptin plays this role in *S. hispidus* I saw no direct relationship between SLC and the scrotal condition in males.

I was surprised to find that SLC did not increase with pregnancy, because leptin is produced by the placenta and plays a role in regulating energy allocation during pregnancy and lactation (Margetic et al. 2002; Zhang and Wang 2008). Maternal plasma leptin levels are known to increase during pregnancy in many mammals, including humans, sheep, bats, and laboratory rats and mice (Zhang and Wang 2008). The lack of

effect may have been caused by low sample size (only 6 females were found pregnant) or the test was confounded by high SLC in females that were pregnant but not visibly so (McCravy and Rose 1992).

Prediction 3: Correlation of Mass and Serum Leptin Concentration

In both sexes body mass limited SLC. This is evident because as body mass increased, it was the 90th percentile of SLC, not central tendency, which increased (Cade and Noon 2003). In other species, SLC is strongly correlated with body fat (Frederich et al. 1995; Hissa et al. 1998; Landt et al. 1998). Because most leptin is secreted by adipose tissue, and body mass is directly correlated with adiposity, I expected SLC to attain higher values with increased body mass. Variance in SLC beneath the 90th percentile could have been caused by unmeasured factors, such as short term fasting, recent or cryptic lactation in females, variance in mass unrelated to adiposity, and residuals in the relationships between energy balance, fat mass, and SLC. The institutional animal care and use committee would not permit me to destructively measure body fat or to house wild-captured animals for a controlled experiment, so I could not directly quantify the relationship between SLC and body fat in *S. hispidus*.

Predictions 4, 5, and 6: Habitat Effects on Mass and Serum Leptin Concentration

Animals in open habitats with less grass cover and more cover by forbs were larger than animals caught in dense grass cover. Body mass dependence on habitat quality was similar in both sexes. This was surprising both because grasses are the primary calorie source of *S. hispidus*, and because predation risk from raptors increases with both body size and habitat openness (Kotler et al. 1988). The greater nutritional

quality of dicot forbs may explain why animals captured in that habitat were larger. In many habitats cotton rats will expend effort to search for dicots to add to their mostly grass diet or will occupy mixed grass-dicot patches (Randolph and Cameron 2001; Cameron et al. 2009). Association between animal mass and bare ground is harder to explain. Cotton rat population density was negatively associated with bare ground (Chapter 3), and denser populations contain more young individuals because of local recruitment from reproduction. Odum (1955) and Goertz (1965) also found that cotton rat body masses tend to correlate negatively with population density. Although I found that *S. hispidus* densities increased with grass cover (Chapter 3), the negative effect of grass cover on mass was probably not caused by intraspecific interactions. Even large *S. hispidus* populations consume a small proportion of NPP in grasslands (Petryszyn and Fleharty 1972; Fleharty and Choate 1973) so if there is intraspecific competition in dense populations, it is for space rather than food.

Among all animals there was no significant relationship between grass cover and any part of the distribution of SLC. Instead, I found that SLC was limited (90th percentile) by forbs and its median decreased with bare ground. Dicotyledonous forbs tended to have a lower C:N ratio as well as a higher protein, lipid, digestible carbohydrate, and more energy overall than monocotyledonous grasses (Randolph et al. 1991; Cameron et al. 2009). This difference in nutrient quality is probably caused by the higher C:N ratio and indigestible lignin in C_4 grasses (Murphy et al. 2002; Barbehenn et al. 2004). Other studies (Randolph et al. 1991, 1995) found that dicot forbs provided better overall nutrition to *S. hispidus* than local grasses and as such should be included in the diet of reproductive females. This may explain why SLC, an indicator of satiety and

energy balance, was limited by dicot forbs rather than grasses. Grasses do provide nutrition to *S. hispidus* (and are their primary food) but multiple lines of evidence now suggest that grass is overall a suboptimal food. The negative relationship between median SLC and bare ground was expected. Ground devoid of vegetation is ground devoid of edible plant matter, so a negative effect on SLC makes sense. The effect of bare ground on median SLC was smaller than the effect of forb cover (Table 19).

When the sexes were analyzed separately, I found that the distribution of SLC in females and males responds differently to habitat quality. In females, the 30th percentile of SLC distribution decreased with increasing cover by grasses. As grasses provide poorer nutrition than other plant sources, female satiety and energy balance may respond more to nutritional quality than overall caloric abundance. Because SLC covaries weakly with mass, it may be that the reason why the relationship between SLC and plant cover in females was only seen near the bottom of the SLC distribution is because smaller female *S. hispidus* are more sensitive to differences in environmental nutrition than larger females (Slade et al. 1996). In males, SLC was limited both by grass cover and forb cover; i.e., by availability of any type of food. This implies that for male *S. hispidus*, nutritional quality of forage is less important than its overall quantity.

I suggest that the sexual dimorphism in physiological response to habitat quality was caused by the nutritional demands of reproduction. Male SLC was limited by availability of food regardless of nutritional quality, whereas female SLC values were lower when grasses were the dominant vegetation. Randolph et al. (1995) found that female cotton rats include dicot forbs in their diet during reproduction, and suggested that this behavior supports the greater need for lipids and proteins during pregnancy. I found

no relationship between female SLC and dicots, but this could have been an effect of low sample size. Limitation of male SLC by any type of food regardless of reflects the lesser investment in reproduction by males compared to females.

A shortcoming of this analysis is that it is impossible to know how much animals had consumed before being captured, how long animals were in traps before blood samples were taken, when they consumed the bait in the trap, and consequently how SLC may have been affected by recent feeding or starvation. The half-life of leptin in *S. hispidus* is unknown. Plasma leptin half-lives reported in other species include 5.5 ± 0.2 min (lean *Rattus*) and 7.0 ± 0.8 min (obese *Rattus*; Vilà et al. 1998), 9.4 ± 3.0 min (*Rattus*; Zeng et al. 1997), 24.9 ± 4.4 min (humans; Klein et al. 1996), and 204 ± 90 min (humans; Wong et al. 2004). Hill et al. (1998) found that leptin in *Rattus* was cleared from plasma in two waves. An initial pool of leptin was cleared with a half-life of approximately 3.4 min. A second pool of leptin which had bound to hypothalamic and peripheral receptors showed a half-life of approximately 71 minutes. If leptin half-life in *S. hispidus* is comparable to leptin half-life in *Rattus*, then the SLC could have been near baseline for individuals that were captured and consumed the bait early in the night. Assuming the longer *Rattus* half-life (71 min), 9 hours in the trap following capture and bait consumption shortly after sunset would leave time for 7.6 half-lives, or a removal of more than 99% of leptin from the blood. A controlled study of leptin kinetics in *S. hispidus* is needed to interpret these findings.

Prediction 7: Abundance Reduces Serum Leptin Concentration

If animals were diverting time from foraging to competing for space, then I should have observed negative relationships between abundance and both SLC. But, I

observed no such relationships (Tables 17–19). Instead, SLC was limited by food availability in the more territorial sex (males; Cameron 1995). This finding, that energy balance of males is affected by food availability rather than abundance of other animals, further suggests that intraspecific interactions did not drive SLC. It could be that the population densities I observed were not high enough to cause intraspecific limitation of mass.

Leptin as an Indicator of Energy Balance

This study is the first examination of leptin in wild *S. hispidus*. I measured SLC partly to evaluate it as a relatively non-invasive indicator of energy balance in wild mammals. Many morphological and chemical indicators of energy balance have been tested (Homyack 2010) and all carry drawbacks that make them less than ideal. Serum leptin concentration is no exception. Studies in laboratory animals have consistently shown a relationship between adiposity (and thus positive energy balance) and SLC. Although I found that body mass does limit SLC, residual variance in the mass-SLC relationship shows that factors other than food intake and nutrition can influence SLC in wild animals. This is not surprising, considering the myriad complex interactions between leptin secretion and other bodily processes (Margetic et al. 2002). Some of this variance may be explained by thermoregulatory challenges (Yang et al. 2011), reproduction (Zieba et al. 2005), or seasonal trends in SLC related to hibernation (Hissa et al. 1998). Nevertheless, I suggest that SLC can be used as an indicator of energy balance in some circumstances. First, the researcher must clearly define what question is being addressed by SLC measurement, and second, effects of season, sex, and reproductive status must be accounted for. In addition, interpretation of SLC (or any

blood parameter) from wild mammals should be supported by data from controlled feeding trials. More study of SLC in *S. hispidus* is needed to elucidate the relationship between nutrition and SLC. It would also be interesting to investigate whether seasonal patterns in SLC exist in *S. hispidus* as they do in other species and whether these seasonal patterns vary with latitude.

Acknowledgments

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CHAPTER FIVE

Small Mammal Edge Responses in Mixed Grass Prairie: Effects of Edge Contrast and Resource Distribution

Abstract

I investigated whether small mammals in a mixed grass Grand Prairie community responded to two types of habitat boundaries: edges where grassy habitat met dicot-dominated habitat ("low-contrast") and edges between grassy habitat and wooded patches ("high contrast"). I tested 3 hypotheses: 1) edge effects reflect habitat affinities (i.e., animals avoid edges with unsuitable habitat); 2) edge effects are driven by whether resource distributions are supplementary (resources qualitatively similar, but varying in abundance between habitats) or complementary (different resources in each habitat); and 3) edge response magnitude increases with edge contrast. North American deer mice (*Peromyscus maniculatus*) did not respond to either type of edge and hispid pocket mice (*Chaetodipus hispidus*) responded negatively to high-contrast edge. Hispid cotton rats (*Sigmodon hispidus*) responded negatively to both edge types, and both responses were of similar magnitude. Small mammal edge responses in this system appear to be matrix responses (abundance mapping to preferred habitat type) rather than mapping to supplementary or complementary resources. Serum leptin concentration, a hormonal indicator of energy availability, did not differ between control grids and wooded edge grids, suggesting that the response of *S. hispidus* to wooded edges was not driven by nutrition.

Introduction

Edge effects are the responses of organisms to ecological boundaries. The concept of ecological edges as boundaries between habitat types was introduced by Clements (1905) and has been refined to define terrestrial edges as discontinuities between plant communities and to accommodate individualistic edge responses (Di Castri et al. 1988; Lidicker and Peterson 1999). Edges present gradients in biotic factors, such as vegetative composition, predator abundance, and food abundance, as well as abiotic factors such as vegetative structure, light, temperature, soil moisture, and wind exposure (Cadenasso et al. 2003). From a mobile organism's point of view, an ecological boundary represents a spatial gradient or discontinuity in the availability of resources. Animals responding to habitat edges are often not responding to the discontinuity itself but to the changes in vegetation at the edge (Kingston and Morris 2000; Ries et al. 2004)

The nature of an edge effect depends on the nature of the habitat edge and the ecological setting (Kingston and Morris 2000). Lidicker and Peterson (1999) suggested a two-parted classification of "matrix" and "ecotonal" effects. Edge responses that can be predicted solely by a species' response to the abutting habitats in isolation are matrix effects, while edge responses not predicted by simple habitat associations are ecotonal effects (Figure 1). Matrix effects lack emergent properties and are caused by the mapping of some response variable (abundance, reproductive rates, animal performance, etc.) onto the suitable and less-suitable habitats at the edge. Strayer et al. (2003) described such edge effects as "noninteractive" effects.

Ecotonal effects are characterized by emergent properties in the response variable that differ from patterns in the adjacent habitats. These are also considered "interactive"

effects because interaction between habitats in the edge zone creates a habitat different from habitat on either side (Strayer et al. 2003). Lidicker (1999, p 337) notes that while it may be difficult to distinguish which type of edge effect is being observed, the matrix effect should be the null hypothesis because "it should be possible to make a clear prediction of the resulting edge response knowing the values of the variables in each habitat-type separately, and assessing the degree of blending on the edge." Matrix effects are observed in small mammals where one of the adjacent habitats is unsuitable (Heske 1995). Ecotonal effects have been observed when adjacent habitats present complementary resources. For example, Lidicker et al. (1992) found that adult male *S. hispidus* preferred areas where blackberry (*Rubus betulifolius* Poir.) abutted grassland, presumably exploiting the grassland for food and the *Rubus* thickets for cover. Although this two-part classification scheme assists in understanding edge effects, it is not as helpful at predicting them.

Ries and Sisk (2004) proposed a model (Figure 2) where the nature of edge effects depends on whether resources on either side of a boundary are supplementary (i.e., each habitat contains the same types of resources, but in differing abundance) or complementary (i.e., when each habitat contains different resources required by the organism). In their model, resource complementarity causes positive edge effects on both sides of the boundary. When resources are supplementary, edge responses will be neutral (or nonexistent) when habitats are similar or transitional (i.e., negative in more suitable habitats and positive in the less suitable habitat) when habitats are dissimilar. An important implication of this model is that all species are predicted to show positive, neutral, and negative edge responses, depending on the ecological context of the edge.

This model has performed well in meta-analyses (Ries et al. 2004) and in experimental studies of riparian butterflies (Ries and Sisk 2008) and urban beetles (Noreika and Kotze 2012).

Edge Effects in Small Mammals

Small mammals (< 1 kg) are a ubiquitous and well-established model system for ecological field studies. I studied edge responses by the 3 most abundant small mammal species in a mixed grass prairie preserve: the hispid cotton rat (*Sigmodon hispidus* Say and Ord 1825), North American deer mouse (*Peromyscus maniculatus*), and hispid pocket mouse (*Chaetodipus hispidus*).

Chaetodipus hispidus is a granivorous heteromyid rodent associated with a wide variety of vegetation types (Paulson 1988). In Texas, *C. hispidus* occurs in dry grasslands with friable soils, often at intermediate levels of ground cover with abundant annual forbs (Paulson 1988; Clark et al. 1998; Jones et al. 2003; Stancampiano and Schnell 2004; Kirchner et al. 2011). Previous reports of edge effects in *C. hispidus* are sparse. In Colorado, Bock et al. (2002) found that *C. hispidus* was more abundant in grassland interior plots than plots near the edge of suburban housing development. Also in Colorado, Stanley's research (2010) revealed that *C. hispidus* occurred more often at edges between shortgrass prairie and cropland than in prairie interiors, but the numbers captured (3 and 4 in successive sampling years) were too few to analyze.

Peromyscus maniculatus is found in a wide variety of habitats throughout North America and is usually considered a habitat generalist (Baker 1968; Wywialowski 1987), although within some ecoregions can be a specialist of certain microhabitats (Morris 1996). Their diet is extremely varied, including many types of plant, animal, and fungal

matter (Wolff et al. 1985). Edge responses by *P. maniculatus* vary with ecological situation. Positive edge effects have been reported at shortgrass prairie-cropland edges (Stanley 2010), and forest clearcut edges (Sekgororoane and Dilworth 1995). Edge avoidance has been reported at grassland-suburban development edges (Bock et al. 2002), California coastal sage-scrub to suburban edges (Kristan et al. 2003), and Appalachian forest edges (Menzel et al. 1999). Edge indifference was reported by Fitch (1979), where abundance in transition zones between lichen-grass open habitat and maple-pine forests was not significantly different than interior of either habitat; by Pasitschniak-Arts and Messier (1998) where prairie abutted wetlands, roads, or contrasting vegetation such as cropland or pasture; and by Walters (1991) at clearcut forest edges. Matlack et al. (2008) found that *P. maniculatus* in tallgrass prairie avoided habitats with woody cover. Mills (1996) found that *P. maniculatus* preferred forest-clearcut edges to interior forest habitat, exhibiting an ecotonal effect. The relatively wide niche breadth of *P. maniculatus* may mean that almost any combination of habitats at an edge will offer complementary resources, so edge effects may be very context-dependent.

Sigmodon hispidus is an herbivorous small mammal common throughout the southeastern United States and parts of northern Mexico (Cameron and Spencer 1981). *Sigmodon hispidus* exploits a variety of food sources but its primary food source is grasses (Goertz 1964; Fleharty and Olson 1969; Cameron and Spencer 1981). Cotton rats have been considered both habitat generalists (Golley et al. 1965; Lidicker et al. 1992; Matlack et al. 2008) and specialists of grassland habitats (Baker 1971); this distinction is arbitrary and scale-dependent. Regardless of whether they are considered specialists or generalists, *S. hispidus* is associated with dense grass habitat (Cameron and Spencer

1981) although individuals are known to supplement their diet by including some space in their territories where dicotyledonous forbs are abundant (Cameron and Spencer 2008). The supplementation here is nutritional: dicot forbs are much richer in proteins, lipids, minerals, and soluble carbohydrates than grasses (Randolph et al. 1991). Other habitats on prairie landscapes are unsuitable for *S. hispidus*: individuals are very rarely captured in wooded or non-grassy patches (Wilkins 1995; Hanchey and Wilkins 1998).

Previous studies of edge effects in *S. hispidus* report a variety of results. Lidicker et al. (1992) found that males preferred grassland-*Rubus* edges to interiors of either habitat. Mabry et al. (2003) found cotton rats near grass-pine forest edges more often than in grassland interiors. In a similar study, *S. hispidus* also did not avoid grassland-wooded edges, but when they dispersed from a grassland patch surrounded by forest they were more likely to follow a grassy corridor than cross the grass-forest edge (Bowne et al. 1999). Constantine et al. (2005) found that *S. hispidus* in loblolly pine forest remnants were more abundant at edges between remnant and clearcut habitat. In tallgrass and mixed grass prairies, *S. hispidus* uses grassland, woodland, and mixed habitats, although abundances are higher in grasslands (Wilkins 1995; Matlack et al. 2008).

Hypotheses

Because habitat edges in terrestrial habitats are usually defined by plant community and edge effects arising from resource mapping by animals onto vegetation are widely studied (Lidicker 1999; Strayer et al. 2003), I chose to test the resource distribution hypothesis in this small mammal community. My primary objectives were to determine whether edge effects exist in this mixed-grass prairie small-mammal fauna, and to determine what causes them. I tested two hypotheses, which I refer to as the

habitat association hypothesis and the resource distribution hypothesis. The habitat association hypothesis is that edge responses result from mapping of organisms onto suitable vs. unsuitable habitats (Lidicker and Peterson 1999) or that conditions at an edge reflect the average of conditions in either adjacent habitat (Strayer et al. 2003). Edge responses can therefore be predicted to follow the matrix vs. ecotonal effect framework of Lidicker and Peterson (1999). In the case of matrix effects, species will respond negatively to edges with unsuitable habitat and positively to edges with more suitable habitat. Ecotonal effects will occur if edge responses do not result from the relative suitability of adjacent habitats.

The resource distribution hypothesis (Ries and Sisk 2004) considers resource availability on either side of the boundary. This hypothesis predicts positive responses when resources are complementary (differing in kind) in adjacent habitats and negative or neutral responses when resources are supplementary (differing in abundance). Both hypotheses predict that magnitude (but not direction) of edge responses will vary with edge contrast, the difference between habitats at the edge (Ries et al. 2004; Noreika and Kotze 2012). I based predictions for the 3 most abundant species in our study on published studies of habitat association, resource requirements, and edge effects (Table 20). To test focal species *S. hispidus* response to nutritional resources, I measured serum leptin concentration (SLC), an indicator of energy balance. SLC is limited by food availability in *S. hispidus* (Chapter 4), so I predicted that if foraging benefit drives edge responses, distribution of SLC would shift with directionality of edge responses. In other words, I expected higher SLC values when edge responses were positive and lower SLC values when edge responses were negative. If SLC did not vary with directionality of

edge response, then I could infer that the benefit (or cost) of being in edge habitats was not nutritional.

Table 20. Edge effect predictions under the habitat association hypothesis (HAH) and resource distribution hypothesis (RDH) and observed effects for hispid pocket mice (*Chaetodipus hispidus*), deer mice (*Peromyscus maniculatus*), and hispid cotton rats (*Sigmodon hispidus*). Effect size is abundance (captures per 100 trapnights) in control grid (no edge) subtracted from grass-forbs edge (LC) or grass-forest edge (HC). When responses of opposite sign are predicted, a one-tailed *t*-test was performed for the HAH prediction; for the RDH prediction, the *t* value and df were the same, and the *P* value is 1 minus the *P* value of the test for the opposite effect. Two-tailed *t*-tests were used to evaluate predictions of no edge effect

		Prediction					
Species	Edge	HAH	RDH	Effect ± SE	Tails	*t*	*P*
Chaetodipus hispidus	LC	+	+	0.24 ± 0.50	1 (+)	0.4794	0.3198
	HC	-	+	–0.63 ± 0.32	1 (-)	–1.9626	0.0357
Peromyscus maniculatus	LC	none	+	0.48 ± 0.54	2	0.8773	0.3962[a]
	HC	none	+	1.27 ± 0.93	2	1.3642	0.1957[b]
Sigmodon hispidus	LC	-	+	–3.81 ± 2.13	1 (-)	–1.7905	0.0483
	HC	-	-	–6.03 ± 2.85	1 (-)	–2.1145	0.0272

[a] *P* value for 1-tailed test for positive response is 0.1981

[b] *P* value for 1-tailed test for positive effect is 0.0978

Methods and Materials

Field Data Collection

Field sampling methods were described in Chapters 3 and 4. Small mammals were sampled in 14 weekly trapping sessions from 3 May to 4 August 2011 at the

Lyndon B. Johnson National Grasslands (LBJNG) near Decatur, Wise County, Texas. In each trapping session I set 3 grids of 30 Sherman traps (8 × 9 × 23 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida, USA) each for 3 consecutive nights. Traps were checked each morning, left closed during the day, and collected after the third morning. Each trap was baited with 5 g of crimped oats. Traps which captured an animal were replaced with a clean trap.

I set grids in each sampling session as a block containing 1 replicate of each of 3 treatments: control (CON), low-contrast edge (LC), and high-contrast edge (HC). Control grids were completely within grassy habitat dominated by little bluestem (*Schizachyrium scoparium*) and Indian grass (*Sorghastrum nutans*). Low-contrast grids were set where grassy habitat met dicot forb dominated habitat. High-contrast grids were set at boundaries between grassy habitat and forested patches. Control and low-contrast grids were set in 6 rows of 5 traps, with 5 m spacing between traps. In low-contrast grids, 3 rows were set in grass-dominated habitat and 3 rows were always in dicot-dominated habitat (distance between rows 3 and 4 was sometimes extended to ensure this). High-contrast grids were set in 3 rows of 10 traps, with 1 row following the edge where grass ended and understory vegetation began, and the other 2 rows congruent to the first but 5 and 10 m away. Preliminary sampling at another prairie preserve (Clymer Meadow, Hunt Co., Texas) showed that boundary effects of wooded patches were usually confined to approximately 20 m from the grass-trees boundary (Chapter 2). Previous studies have also found that small mammals may have little capacity to detect landscape-level features at distances ≥ 30 m (Zollner and Lima 1997). All procedures involving live animals were approved by the Baylor University Animal Care and Use Committee and

were in accordance with the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011). Sampling was carried out under a Texas Parks and Wildlife Scientific Collection Permit and a United States Forest Service Special Use Permit.

Blood Samples and Leptin Assays

Procedure for sampling SLC was described in Chapter 4. I took a blood sample of between 50 to 300 μL from the saphenous veins of cotton rats weighing ≥ 30 g. Only 1 sample was taken from each individual, even if the animal was recaptured on a subsequent day. I shaved a hindlimb, swabbed the skin with isopropanol to reduce the probability of infection, and punctured the saphenous vein with a sterile 21 or 23 gauge hypodermic needle. Blood was collected with a 300 μL capillary blood collection tube (Microvette™ 300 Serum, Sarstedt AG & Co., Nümbrecht, Germany). Blood samples were centrifuged at 2000 × *g* for 15 minutes and serum was pipetted off and stored in a clean microcentrifuge tube. Samples collected on the first 2 mornings of a session were stored at 0 °C near the field site; on the last morning of each session I returned to the laboratory and stored all blood samples at –80 °C until analysis. Samples were kept at or below 0 °C during transit.

I quantified SLC using enzyme-linked immunosorbent assay (ELISA) for rat leptin (Invitrogen Corporation, Camarillo, California, USA). SLC of unknown samples were compared to a standard curve (3 parameter logistic) generated from known concentrations of 0, 62.5, 125, 250, 500, 1000, 2000, and 4000 pg/mL purified *E. coli*-expressed recombinant Rt leptin. The mean of 2 duplicates was used for all standards

and for most samples (some samples were large enough for only one assay). All samples were within the detectable range of leptin (250 to 16×10^3 pg/ml).

Data Analysis

I used relative abundance (captures per 100 trapnights) to analyze rodent abundance. I considered the 3 grids set in each session to be a block. Within each block I calculated the effect of each edge type by subtracting abundance in the control grid from abundance in an edge grid. I used one-tailed or two-tailed *t*-tests to test for a significant edge effect. One-tailed tests were used when a directional edge response was predicted, whereas two-tailed tests were used when no edge response was predicted (Table 20). If a species responded to both edge types, I used a paired *t*-test to determine if the mean response was the same for both treatments. I pooled SLC data across blocks because only 2 sessions had > 1 SLC sample in every grid type. Instead I used the two-sample Kolmogorov-Smirnov test to determine whether the underlying empirical distribution function of SLC differed between grid types (Pacheco and Henderson 1996). All statistical analyses were performed in R version 2.13.1 (R Development Core Team 2011). Standard curves for leptin analyses were fit using R package drc version 2.2–1 (Ritz and Streibig 2005). I used Anscombe-Glynn tests in package moments version 0.12 to evaluate kurtosis of SLC distributions (Komsta and Novomestky 2011).

Results

Relative Abundance

Summary of capture rates in each grid type is shown in Table 21. Mean capture rate per grid was 8.2 captures per 100 trapnights ± 1.1 SE, ranging from 0 to 26.6

Table 21. Summary of abundance data for small mammals in 3 treatments, 2011. Overall abundances and occurrences presented in line with binomen

Species	Grids present	Relative abundance		
		Mean ± SE	Median	95% CI of Median
Sigmodon hispidus	29	6.2 ± 1.1	3.3	1.1 – 7.8
Control	12	9.4 ± 2.3	7.5	1 – 16
Low-contrast	11	5.6 ± 1.8	2.5	2.5 – 11
High-contrast	6	3.4 ± 1.2	0.0	0 – 7
Peromyscus maniculatus	12	1.0 ± 0.3	0.0	0 – 0
Control	2	0.4 ± 0.3	0.0	0 – 0
Low-contrast	5	0.9 ± 0.4	0.0	0 – 2
High-contrast	5	1.7 ± 0.8	0.0	0 – 3
Chaetodipus hispidus	13	0.7 ± 0.2	0.0	0 – 0
Control	6	0.8 ± 0.3	0.0	0 – 2
Low-contrast	5	1.0 ± 0.5	0.0	0 – 3
High-contrast	2	0.2 ± 0.1	0.0	0 – 0
Peromyscus leucopus	3	0.1 ± 0.1	0.0	0 – 0
Control	1	0.1 ± 0.1	0.0	0 – 0
Low-contrast	0	0.0 ± 0.0	0.0	0 – 0
High-contrast	2	0.2 ± 0.1	0.0	0 – 0
Reithrodontomys fulvescens	9	0.3 ± 0.1	0.0	0 – 0
Control	5	0.6 ± 0.3	0.0	0 – 1
Low-contrast	3	0.2 ± 0.1	0.0	0 – 1
High-contrast	1	0.1 ± 0.1	0.0	0 – 0

captures per 100 trapnights. I detected no spatial autocorrelation between grids with respect to rodent abundance (|Mantel's r| < 0.08, $P \geq 0.14$ for all species), nor temporal autocorrelation (|Mantel's r| < 0.04, $P \geq 0.26$ for all species). I attempted to analyze edge effects only in *S. hispidus*, *P. maniculatus*, and *C. hispidus* because capture rates in *P. leucopus* and *R. fulvescens* were too small.

Chaetodipus hispidus responded negatively to grass-forest edges (high-contrast) and did not respond to grass-forb edges (low-contrast; Table 20; Figure 20). *Sigmodon hispidus* responded negatively to both types of edges (Table 20; Figure 20), and the magnitude of responses was not significantly different between edge types (t = 0.9309, 13 df, P = 0.3689). *Peromyscus maniculatus* did not respond to any kind of habitat edge. A one-tailed t-test for the expected positive effect was not significant (Table 20; Figure 20).

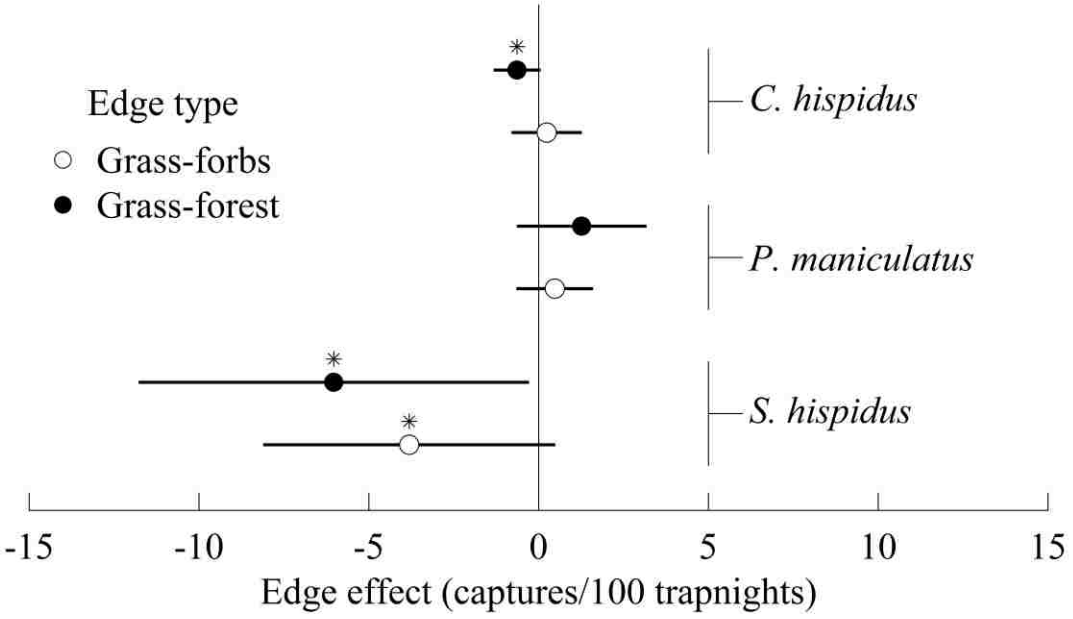

Figure 20. Forest plot of within-block edge effects for *Chaetodipus hispidus*, Peromyscus *maniculatus*, and *Sigmodon hispidus*. Edge effect is defined as difference in abundance between grass-dicot edges and control grids (open symbols) or between grass-woods edges and control grids (closed symbols) in each sampling session. Symbols and lines show 95% CI ($\bar{x} \pm 2$ SE), and asterisks denote significant edge effects (Table 20)

Serum Leptin Concentration in Sigmodon hispidus

Summary SLC data are shown in Table 22. Among all animals, SLC did not differ between treatments (Kruskal-Wallis $\chi^2 = 0.89$, 2 df, $P = 0.64$), nor among males (Kruskal-Wallis $\chi^2 = 0.08$, 2 df, $P = 0.96$), nor among females (Kruskal-Wallis $\chi^2 = 1.39$, 2 df, $P = 0.49$). The underlying distribution function of SLC did not differ between control and low contrast grids ($D = 0.13$, $P = 0.92$) or between control and high contrast grids ($D = 0.23$, $P = 0.45$); there were also no differences when sexes were analyzed separately ($P > 0.4$ in all comparisons; Figure 21). Distribution of SLC was significantly leptokurtic in control grids ($z = 2.65$, $P < 0.01$) and high-contrast grids ($z = 2.18$, $P = 0.03$). When sexes were analyzed separately, the SLC distribution was significantly leptokurtic among males in high-contrast grids ($z = 2.71$, $P < 0.01$).

Table 22. Summary data for serum leptin concentration (SLC; pg/ml) in hispid cotton rats (*Sigmodon hispidus*) in each treatment. One animal of unrecorded sex captured in a control grid is included with all animals for that treatment

Grid type	Animals	*n*	$\bar{x} \pm$ SE
Control	All	44	1019 ± 37.0
	Females	14	1117 ± 51.8
	Males	29	955 ± 48.1
Low-contrast	All	28	1007 ± 35.9
	Females	8	993 ± 75.8
	Males	20	1010 ± 41.1
High-contrast	All	21	1041 ± 43.8
	Females	11	1134 ± 74.1
	Males	10	972 ± 45.0

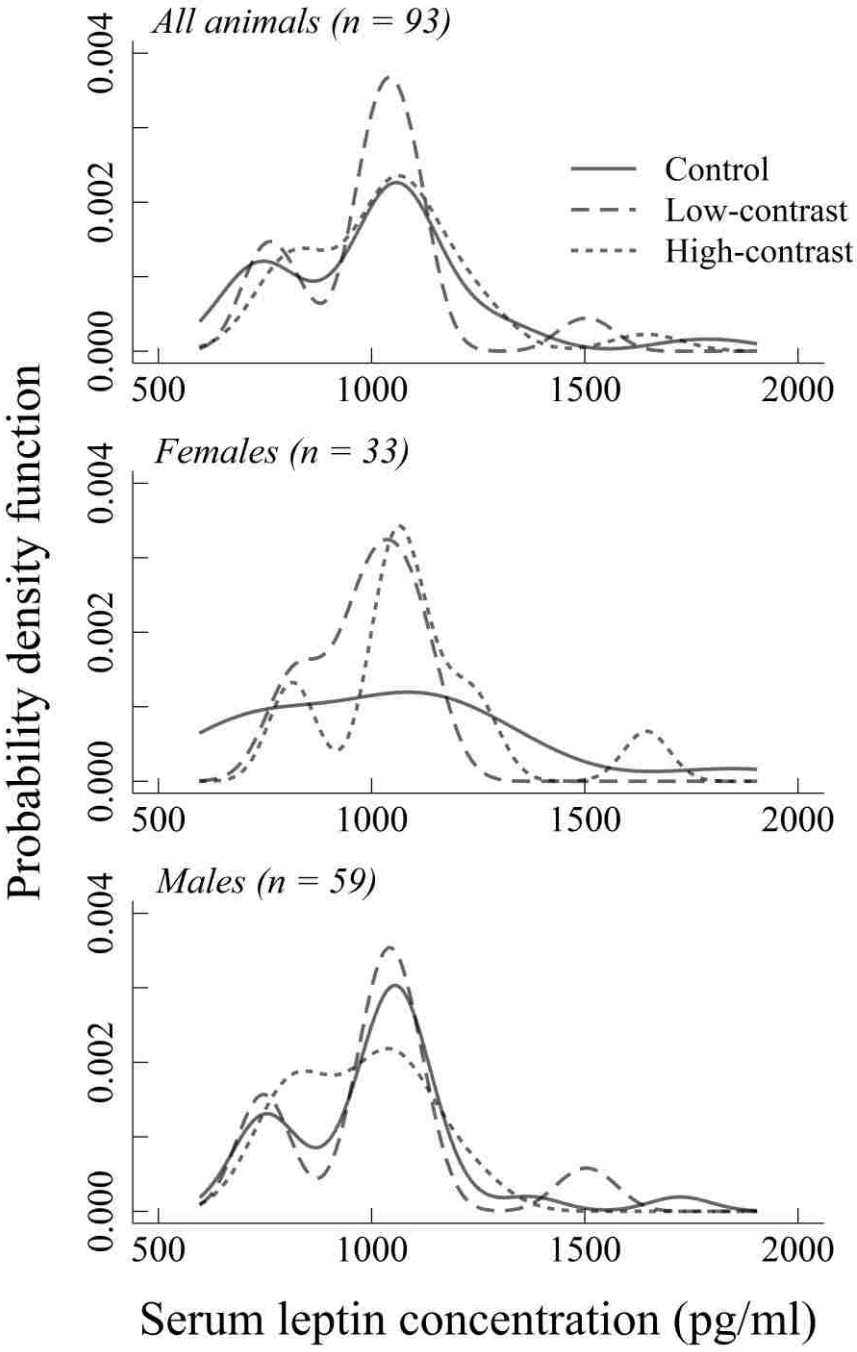

Figure 21. Distribution of serum leptin concentration (SLC; pg/ml) in hispid cotton rats (*Sigmodon hispidus*) in control grids (grassy interior), low contrast grids (grass-dicot forb edge), and high contrast grids (grass-forest edge). Y-axis shows the probability density estimate for a given value of SLC

Discussion

Predictions 1 and 2: Edge Effects in Chaetodipus hispidus *and* Peromyscus maniculatus

I found a significant negative response by *C. hispidus* to grass-forest edges and no response to grass-forb edges (Figure 20). This species is known to favor habitats with dense annual forb cover and intermediate overall cover, although its tolerance for disturbance varies with ecological situation (Paulson 1988; Clark et al. 1998; Jones et al. 2003; Stancampiano and Schnell 2004; Kirchner et al. 2011). Because of this I thought that habitat associations alone would predict a positive response to grass-dicot edges and a negative response to wooded edges (Table 20). The prediction by the resource distribution hypothesis of positive response to all edge types was incorrect.

Lack of edge effects in *P. maniculatus* was predicted by the habitat association hypothesis because of this species' generalist habits (Baker 1968; Wywialowski 1987), but not by the resource distribution hypothesis. If the data are interpreted in light of the resource distribution hypothesis, *P. maniculatus* showed a neutral edge response at both edge types because resources were supplementary between grassy and dicot habitats and between grassy and wooded habitats, but did not differ greatly in availability.

Lack of positive edge responses in both *C. hispidus* and *P. maniculatus* could have been caused by an erroneous assumption that these species exploit different resources in grassy habitats than in dicot or wooded habitats in this mixed grass ecoregion. It should also be noted that both *P. maniculatus* and *C. hispidus* were captured in less than one-third of trapping grids and were always present in low numbers (Table 21). Previous reports of edge effects in these species have been based on greater capture rates (Menzel et al. 1999; Bock et al. 2002). Our low capture rate could have

prevented a meaningful analysis of patterns in abundance between groups of grids. In addition, grid types were defined largely by the habitat requirements of our target species, *S. hispidus* and in such a way that they could be easily demarcated in the field. Both of these decisions may have led to the examination of edge types that are not relevant to *C. hispidus* or *P. maniculatus* (although I doubt that any species of small mammal does not perceive starkly contrasted grass-forest boundaries). Lack of edge effects could also mean that *C. hispidus* and/or *P. maniculatus* selects habitat at spatial scales larger than those examined in this study (Morris 1987).

Predictions 3 and 4: Edge Effects in Sigmodon hispidus

In a previous analysis (Chapter 3) I found that cotton rats associated with dense grass cover while avoiding nongrass vegetation and bare ground. Those habitat affinities were reflected in the response of *S. hispidus* to habitat edges. Abundance of *S. hispidus* was highest in grids dominated by grasses only (control grids) and lowest in grids where grassy habitat abutted wooded patches (Table 21). The competing hypotheses predicted opposing responses to grass-forb (low-contrast) edges: either a negative response because *S. hispidus* is a specialist of grassy habitats, or a positive response to grass-forb edges because of the complementary resources available in grass-dominated and forb-dominated habitats. I observed a weak negative response. This suggests that *S. hispidus* in this ecosystem exhibits matrix edge effects rather than ecotonal effects (Lidicker and Peterson 1999). Kingston and Morris (2000) found a similar lack of ecotonal effects in red-backed voles (*Clethrionomys gapperi* (Vigors 1830)) at edges between conifer forest and logged (approximately 15 y before trapping) habitat and concluded that any apparent edge effects were really responses to local differences between habitat (i.e., a matrix or

noninteractive edge effect). Both hypotheses can explain the negative effect of high contrast edges. The habitat association hypothesis suggests that *S. hispidus* are less abundant near the edges of habitat patches because of resource mapping and/or local demographic history. Under the resource distribution hypothesis, a negative edge response implies either that resources are much less abundant in wooded habitat and supplementary to resources in grassy habitat, or that wooded habitat is simply unsuitable for cotton rats.

I had expected that greater edge contrast would cause a greater edge response, but found that the response of *S. hispidus* to wooded edges was not significantly greater than its response to the lower-contrast grass-forb edges and that contrast increased the likelihood of response by *C. hispidus*. Edge response increasing with edge contrast has been found in grassland bobolinks (Fletcher and Koford 2003), carabid beetles in Finnish forests (Noreika and Kotze 2012), farmland birds (Reino et al. 2009) and in Siberian flying squirrels (*Pteromys volans*; Desrochers et al. 2003). In the context of the resource distribution hypothesis, these negative responses imply that the resources available in wooded and forb-dominated patch types are supplementary to resources available in grassy patches (Ries et al. 2004).

Effects of Habitat Edges on Serum Leptin Concentration in Sigmodon hispidus

Neither the central tendency nor the distribution shape of serum leptin concentration (SLC) differed between control grids and either type of habitat edge (Figure 21). The implication of this finding is that the overall nutritional benefit of foraging does not differ between grassy interior habitat and habitat where grass abuts other habitats. Food availability limits SLC in male *S. hispidus* and affects the lower

envelope of SLC distribution in *S. hispidus* females (Chapter 4). As such, I expected that a shift in the distribution of SLC in one treatment relative to another could indicate where animals were gaining the most nutrition, and suggest whether a difference in abundance (such as between control grids and wooded-edge grids) was caused by differential foraging success in one type of grid or another. The finding that abundance of *S. hispidus* responded negatively to wooded edges, without a congruent pattern in SLC, suggests that nutrition does not cause edge effects in *S. hispidus*. If resource distribution drives edge effects in *S. hispidus*, the key resource may be cover rather than nutrition because while cover varies in abundance between grassland and woodland habitats, available forage (i.e., floristic composition) also varies in kind. Other studies have found that dense grass cover is also important to *S. hispidus* as shelter from predators and as nesting material (Goertz 1964; Cameron and Spencer 1981).

Comparison of Hypotheses

I found little evidence for ecotonal effects in the small mammal fauna of this Grand Prairie ecosystem. Instead, edge responses largely correspond with habitat associations. I found that the habitat association hypothesis, where animals avoid boundaries with unsuitable habitat regardless of mechanism, performed slightly better than the resource distribution hypothesis. Whenever the predictions of the hypotheses differed, the habitat association hypothesis was correct (Table 20). However, 2 of those 4 predictions were predictions of no edge response by *P. maniculatus*. Given the low capture rate of *P. maniculatus*, correctly predicting a non-effect can hardly be considered strong support. Low capture rates of *C. hispidus* and *P. maniculatus* may have confounded the analysis. Future work on any mechanism of edge effects in small

mammals should sample locations more thoroughly. Because avoidance of wooded boundaries by *S. hispidus* was predicted by both the habitat association and resource distribution hypotheses, I cannot determine which hypothesis is better for predicting edge responses by *S. hispidus*. Similar SLC values in all grid treatments suggest that *S. hispidus* response to wooded edges was not caused by nutrition, but instead by other effects of wooded patches infiltrating the grassland, such as vegetative cover, light, temperature, or interspecific interactions. Future studies of edge responses in *S. hispidus* can clarify which resources drive edge effects.

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CHAPTER SIX

Conclusions

Dissertation Questions

Findings of this dissertation are organized below by questions as presented in Chapter 1.

Dissertation Question 1: Habitat Association

Hypothesis. Every species has unique resource and space requirements, so small mammal species should be associated with particular habitat types. When a species is found, it should be associated with some habitats more than others. This association could be continuous (abundance correlated with some measure of habitat quality) or discrete (abundance differs between habitat types).

Findings. In Chapter 3 I showed that the relative abundances of three species, *C. hispidus*, *P. maniculatus*, and *S. hispidus*, each map differently to the plant cover types found in a mixed grass prairie preserve. *Sigmodon hispidus* was most abundant in microhabitats with dense grass cover and *P. maniculatus* was most abundant in microhabitats with intermediate forb and bare ground cover and trees. *Chaetodipus hispidus* was associated with intermediate levels of grass cover. In addition, *S. hispidus* avoided heterogeneous habitats, while *P. maniculatus* preferred them. The contrasting responses to habitat heterogeneity reflect the grassland specialization of *S. hispidus* and generalist habits of *P. maniculatus*. Though these findings generally agree with previous literature, they suggest that plant cover heterogeneity at small spatial scales (tens of

meters) exerts strong influence on rodent abundance and diversity. Because many habitat edges present very short gradients, it follows that the changes in plant cover at edges should provoke edge responses by small mammals.

Dissertation Question 2: Edge Effects as Matrix Effects

Hypothesis. If edge effects result from the meeting of suitable habitat and unsuitable habitat (i.e., matrix), then edge responses should be negative when compared to interior habitat and positive when compared to matrix interior (habitat association hypothesis; Lidicker and Peterson 1999). Put another way, edge responses should reflect simple habitat associations. This hypothesis was also put forward by Ries and Sisk (2004).

Findings. The species which was mostly likely to show edge responses in any year at any field site, *S. hispidus*, always responded negatively to edges where grassy habitat abutted wooded patches. This is attributable directly to the widely known specialization of *S. hispidus* for dense grass cover (Goertz 1964; Cameron and Spencer 1981) and suggests that wooded patches in prairie landscapes act as matrix habitat for *S. hispidus*. Sampling at another prairie preserve found that while other species (*P. maniculatus*, *R. fulvescens*) would occasionally use (but not completely cross) wooded drainages that separated prairie plots, *S. hispidus* were never captured in these habitats, were rarely captured near them, and were never documented to cross them (Kirchner et al. 2011). Other studies have found that *S. hispidus* will readily cross grassland-woodland boundaries (Bowne et al. 1999, Constantine et al. 2005).

Dissertation Question 3: Edge Effects as Ecotone Effects

Hypothesis. If the meeting of two habitat types creates a distinct "edge habitat", then edge responses should have the same sign on both sides of an edge (i.e., abundance in edge habitat is higher than or lower than both habitat and matrix interiors). Lidicker and Peterson (1999) call this an "ecotonal effect."

Findings. In 2009 and 2010 I trapped both interior grassland habitat and interior wooded habitat, and observed no evidence of ecotonal edge responses. Every response to high contrast edges is better understood as a matrix effect (Lidicker and Peterson 1999) or a transitional effect (Ries et al. 2004); every response to low contrast edges is congruent with a neutral or transitional response (Table 20). Ecotonal responses by small mammals have been observed (Lidicker et al. 1992; Mills 1996) in other ecoregions. The preponderance of matrix effects on *S. hispidus* abundance in these tallgrass and mixed grass prairie ecoregions may result from the high suitability of grasslands and high unsuitability of wooded habitats. This suggests that when contrast at an edge is too great, habitat difference overrides resource complementarity. It is difficult to draw strong conclusions about the edge behavior of other species in this study because they were captured so infrequently.

Dissertation Question 4: Edge Effects as Resource Mapping, and
Dissertation Question 9: Endocrine Signal of Resource Mapping in Sigmodon hispidus

Hypothesis. 4. Edge responses are determined by the distribution of resources on either side of an edge (Ries and Sisk 2004). Small mammals should respond to edges negatively when the resources in another habitat are supplementary to those in their own

habitat, and should respond positively when resources in another habitat are complementary to those in their own habitat.

Hypothesis. 9. If the resource that drives edge responses by *S. hispidus* is nutrition, then SLC should vary between edge habitats and interior habitats.

Findings. It is difficult to disentangle the influence of habitat structure (i.e., plant cover that defines habitats and thus edges between them) and the influence of resource availability in different habitats. In this study I attempted to measure resource availability indirectly by measuring organism performance. Serum concentrations of the hormone leptin, known in other species to correlate with fat mass and energy intake, did not differ between *S. hispidus* found in grassland interiors and *S. hispidus* found near habitat edges. This finding (Chapter 5), coupled with the numerical responses by *S. hispidus* to plant cover (Chapter 3) and edges (Chapter 2, Chapter 5), and the limitation of SLC by body mass and food availability (Chapter 4), suggests that the resources that differ between these habitats are not nutritional resources. Instead, other resources that differ between grassland and wooded patches drive *S. hispidus* edge responses. Cover from predators and microclimate are two such factors.

Dissertation Question 5: Alteration of Edge Effects by Habitat Contrast

Hypothesis. If edge effects are caused by a difference in habitat suitability or resource availability, then the magnitude of an edge effect should depend on the degree of difference between habitats.

Findings. I addressed this question in two ways. In pilot sampling (Chapter 2) I evaluated several methods of condensing the steepness of a multivariate plant cover gradient into a single metric. While the metrics based on a distance matrix performed well at separating edge types, they were very poor predictors of rodent abundance. In fact, these metrics predicted edge responses in the opposite direction as those actually observed: models showed that *S. hispidus* abundance increased with increasing values of contrast metrics.

The second, and more informative, way was to compare the response of species to two different kinds of edges with different degrees of contrast. The first class of edges, low contrast edges, were boundaries between grassland and large patches of dicot forbs. The second class of edges, high contrast edges, were boundaries between grassland and wooded patches. When edge responses were observed, the two classes of edges provoked responses that were similar in direction but potentially differing in magnitude.

Dissertation Question 6: Effect of Mass on Serum Leptin Concentration in Sigmodon hispidus

Hypothesis. If the hormone leptin is produced by adipose tissue and tied to overall energy intake, then serum leptin concentration (SLC) should vary with animal mass.

Findings. The relationship between body mass and leptin was more complicated than expected. While controlled studies in laboratory animals showed simpler relationships, many factors in the field likely obscured the relationship between mass and SLC. SLC was also shown to vary with food availability (Chapter 4), and interactions

between habitat quality, animal health, and season could have influenced the distributions of SLC that I found.

Dissertation Question 7: Sexual Dimorphism in Serum Leptin Concentration

Hypothesis. If the hormone leptin is produced by adipose tissue, then the more adipose sex should have the highest SLC.

Findings. I found no evidence that SLC varied between the sexes, and no evidence that the relationship between SLC and mass varied between the sexes. My original plan was to conduct controlled feeding trials and subsequently measure SLC and body fat percentage directly. While this would have better elucidated the relationship between mass, sex, fat mass percentage, SLC, and other organismal variables in *S. hispidus*, the Animal Care and Use Committee would not allow this experiment to be performed in the Baylor animal care facility because we lack the appropriate USDA permits to house wild-captured mammals.

Dissertation Question 8: Relationship between Leptin and Food Availability

Hypothesis. If the hormone leptin is produced by adipose tissue and tied to overall energy intake, then serum leptin concentration should vary with food availability in an organism's environment. For *S. hispidus*, the species of interest, food availability is indicated by the density of grasses and dicot forbs.

Findings. I found that SLC was limited by food availability in males but not in females. In females, the pattern was less clear. This suggests that for males, the

availability of nutrition, regardless of quality, is the primary determinant of growth rates and body size. Because females must occasionally acquire additional minerals, amino acids, and lipids to support a pregnancy, they might need to be more selective about their diet. Previous studies (Randolph et al. 1991; Cameron and Spencer 2008) have found that female *S. hispidus* accomplish this by including dicot forbs in their diet. I found no relationship between female SLC and forb cover but did observe that the lower envelope of SLC in females declined with cover by less nutritious grasses. More study of the comparative physiology and foraging ecology of female and male *S. hispidus* is needed.

Conclusions

As natural areas are increasingly fragmented by human activity, edge effects will become more important for conservation. The effects of habitat edges on landscapes can be profound. Many apparent effects of habitat areal loss can actually be ascribed to increased prevalence of edge habitats (Ewers et al. 2007; Banks-Leite et al. 2010). Although the species I studied are of little conservation concern, the results of this dissertation could inform decisions about land management for threatened or endangered small mammals.

In this prairie small mammal fauna, edge contrast appears to affect the likelihood rather than the magnitude of edge responses. My findings show that conservation of edge-sensitive small mammals should include management of edge contrast, by minimizing sharp habitat boundaries. Edge effects on small mammals in these tallgrass and mixed grass prairie ecosystems appear to be relatively uncomplicated, with abundances in edge zones reflecting transitions between habitat and non-habitat rather than emergent edge properties.

Other findings of this dissertation relate more specifically to hispid cotton rats. I found that the primary extrinsic influence on population sizes was not food availability, but rather overhead cover (overhead from the perspective of a cotton rat). While *S. hispidus* abundance generally mapped availability of one food (grass density), it decreased with non-grass ground cover even when that non-grass cover was a valuable food source. Dicot-dominated patches had more open ground, suggesting that the absence of cover is more influential than the presence of food. Examination of serum leptin concentration (SLC) confirmed this suspicion. While SLC in individuals was limited by food availability (especially in males), increase in available nutrition (grasses and dicot forbs) was not always reflected in increased population size. Abundance and available food only covaried when the food source (grasses) also offered dense cover. The broader application of this finding is that conservation may require close attention to fine-scale habitat structure and not just large-scale availability of resources.

Directions for Future Study

Although some light has been shed on the mechanisms that drive edge responses by small mammals, there are questions that merit future study:

1. What is the Influence (or Influences) of the Matrix?

I considered the most prevalent habitat type, little bluestem dominated grassland, to be interior habitat and studied how inhabitants of those grasslands responded to boundaries with other habitats. It would be interesting to sample more extensively inside wooded patches on these prairie landscapes to better quantify their suitability for the

grassland species and to study more closely the climatic, edaphic, or faunal influences of the wooded or dicot habitats on the grassland.

2. How Closely Does Serum Leptin Concentration Track Energy Intake and Availability in Sigmodon hispidus*?*

A lack of permits prevented me from conducting a planned laboratory feeding trial to measure how precisely serum leptin concentration (SLC) might be tied to energy intake. In lieu of that experiment I had to measure the SLC-energy relationship indirectly (Chapter 4). An important follow up to this dissertation would be a controlled feeding experiment where cotton rats were randomly assigned to feeding treatments of varying nutritional content, their intake monitored, and successive blood samples taken to measure if (and if so how) SLC changed between rats in subsistence (low energy) and Western (high energy) diets.

3. Do Population Processes Affect Edge Responses?

An alternative interpretation of the findings from 2009 and 2010 is that edge responses by *S. hispidus* are density dependent. In the high abundance year (2009) edge effects were detected, while in the low abundance year (2010) no effects were detected. I also found that cotton rat masses were smaller in habitats where abundance was highest (Chapter 4). This is probably caused by a greater number of young animals resulting from local recruitment. Given that *S. hispidus* populations are heavily dependent on local recruitment and density dependent regulators such as parasites (Goertz 1964), the apparent response to edges may represent a fitness penalty in edge habitats. Therefore, reduced abundance at edges may reflect local reproductive rates rather than habitat

selection. Longer term tracking of individuals and populations would be required to make such a determination.

4. Do the Matrix Responses Observed in this Study Apply to Other Landscapes?

The existence and nature of edge effects depends on what habitats meet at an edge, how different they are, and perhaps the broader context of that edge on a landscape. Greater diversity of habitats on a landscape, and coarser or finer degrees of fragmentation might influence how small mammals respond to edge. More intensive sampling and more spatially explicit models would be needed to determine if the effects seen in this simple experimental system apply on more complex landscapes.

5. What resources drive small mammal edge responses?

In this study I found evidence that small mammal edge responses are not driven by nutrition. A future study could attempt to manipulate resource availability on one side of an edge and then observing the effects on edge responses. Possible manipulations include: supplementing nutrition on one or both sides of the edge, simulating increased predator density, reducing or increasing cover, or introducing microclimatic changes or light availability.

APPENDIX

APPENDIX

Selected R Code

Script for Determining Habitat Contrast from Vegetation Data

The following script was used to calculate the contrast metrics evaluated in Chapter 2. Comments are marked by ##. An example dataset (tenveg) is shown.

```
## IMPORT PLANT COVER DATA.
> TENVEG <- READ.TABLE(FILE="CLIPBOARD",HEADER=TRUE)
> HEAD(TENVEG)
  GRID ROW TRAP TREAT HAB END BARE BS10 BS25 BS50 SG10 SG25 SG50
1    A   1    2   CON  TG END    0 63.0 63.0  3.0 15.5    3    0
2    A   1    4   CON  TG END    0 63.0 63.0 15.5 15.5    3    0
3    A   2    3   CON  TG MID    0  3.0 38.0 15.5  0.0    0    0
4    A   2    4   CON  TG MID    0 38.0 63.0  3.0  3.0    3    0
5    A   3    1   CON  TG MID    0 85.5 15.5  3.0  0.0    0    0
6    A   3    3   CON  TG MID    0  3.0 38.0  3.0  0.0    0    0
  OG10 OG25 OG50  F10  F25  F50 W25 W50
1 38.0  0.0    0 15.5 15.5  0.0   0   0
2 38.0  0.0    0  3.0 15.5 15.5   0   0
3 38.0  3.0    0 15.5 15.5  3.0   0   0
4 15.5  0.0    0 15.5 38.0 38.0   0   0
5 63.0 15.5    0  3.0  3.0 15.5   0   0
6 38.0  0.0    0  3.0 38.0 15.5   0   0

## NOTE THAT 'TREAT' IS INCLUDED FOR LATER ANALYSES;
## COLUMN 'END' IS TO TELL PART OF THE FUNCTION WHETHER AN
## OBSERVATION COMES FROM THE END OF A GRID OR NOT.

## MAKE SURE THAT PACKAGE VEGAN IS LOADED
## (NEEDED FOR DISTANCE MATRICES)

## MAKE VECTOR OF GRID NAMES, FOR BUILDING THE OUTPUT DATA FRAME.
## TEN IS DATASET OF RODENT DATA, WITH 1 ROW / GRID

TENGRD <- AS.CHARACTER(TEN$GRID)

## MAKE DATA FRAME WITH ALL OF THE COLUMNS THAT WE WANT.
CONTEN <- MATRIX(NROW=51,NCOL=8)
COLNAMES(CONTEN) <-
C("GRID","BCSUM","BCEND","EUSUM","EUEND","SH.MN","SH.SE","SH.SD")
CONTEN <- AS.DATA.FRAME(CONTEN)

## CODE FOR BRAY-CURTIS ALL SAMPLES
FOR (I IN 1:LENGTH(TENGRD)){
      CONTEN$GRID[I] <- TENGRD[I]
      CONTEN$BCSUM[I] <-
ROUND(SUM(VEGDIST(TENVEG[TENVEG$GRID==TENGRD[I],7:21],METHOD="BRAY"))
,2)
```

```
## BRAY-CURTIS ENDS ONLY
## THE CONDITIONALS STORE NA FOR ANY GRID THAT HAS NO ENDS.
## THESE WERE THE GRIDS THAT WERE SET ALONG A GRASS-WOODED EDGE
## RATHER THAN ACROSS THE EDGE.
FOR (I IN 1:LENGTH(TENGRD)){
      CONTEN$GRID[I] <- TENGRD[I]
      IF (TENGRD[I]=="D"){CONTEN$BCEND[I] <- NA}ELSE
      IF (TENGRD[I]=="L"){CONTEN$BCEND[I] <- NA}ELSE
      IF (TENGRD[I]=="DDD"){CONTEN$BCEND[I] <- NA}ELSE
      IF (TENGRD[I]=="EEE"){CONTEN$BCEND[I] <- NA}ELSE
      IF (TENGRD[I]=="GGG"){CONTEN$BCEND[I] <- NA}ELSE
      IF (TENGRD[I]=="HHH"){CONTEN$BCEND[I] <- NA}ELSE
      CONTEN$BCEND[I] <-
ROUND(SUM(VEGDIST(TENVEG[TENVEG$GRID==TENGRD[I]&TENVEG$END=="END",7:2
1],METHOD="BRAY"),NA.RM=TRUE),2)
}
## EUCLIDEAN DISTANCE, ALL SAMPLES
FOR (I IN 1:LENGTH(TENGRD)){
      CONTEN$GRID[I] <- TENGRD[I]
      CONTEN$EUSUM[I] <-
ROUND(SUM(VEGDIST(TENVEG[TENVEG$GRID==TENGRD[I],7:21],METHOD="EUCLIDE
AN")),2)
}
## EUCLIDEAN DISTANCE, ENDS ONLY
FOR (I IN 1:LENGTH(TENGRD)){
      CONTEN$GRID[I] <- TENGRD[I]
      IF (TENGRD[I]=="D"){CONTEN$EUEND[I] <- NA}ELSE
      IF (TENGRD[I]=="L"){CONTEN$EUEND[I] <- NA}ELSE
      IF (TENGRD[I]=="DDD"){CONTEN$EUEND[I] <- NA}ELSE
      IF (TENGRD[I]=="EEE"){CONTEN$EUEND[I] <- NA}ELSE
      IF (TENGRD[I]=="GGG"){CONTEN$EUEND[I] <- NA}ELSE
      IF (TENGRD[I]=="HHH"){CONTEN$EUEND[I] <- NA}ELSE
      CONTEN$EUEND[I] <-
ROUND(SUM(VEGDIST(TENVEG[TENVEG$GRID==TENGRD[I]&TENVEG$END=="END",7:2
1],METHOD="EUCLIDEAN"),NA.RM=TRUE),2)
}
## MEAN OF SHANNON INDEX ON VEGETATION WITHIN A GRID
FOR (I IN 1:LENGTH(TENGRD)){
      CONTEN$SH.MN[I]<-
MEAN(DIVERSITY(TENVEG[TENVEG$GRID==TENGRD[I],7:21],INDEX="SHANNON",MA
RGIN=1))
}
## STANDARD ERROR OF SHANNON INDEX WITHIN A GRID
FOR (I IN 1:LENGTH(TENGRD)){
      CONTEN$SH.SE[I]<-
STDERR(DIVERSITY(TENVEG[TENVEG$GRID==TENGRD[I],7:21],INDEX="SHANNON",
MARGIN=1))
}
## STANDARD DEVIATION OF SHANNON INDEX WITHIN A GRID
FOR (I IN 1:LENGTH(TENGRD)){
      CONTEN$SH.SD[I]<-
SD(DIVERSITY(TENVEG[TENVEG$GRID==TENGRD[I],7:21],INDEX="SHANNON",MARG
IN=1))
}
## END FUNCTION
```

Functions for Computing and Presenting Standard Error

This function was used for computing the standard error of the mean for many groups of data. Because R has no built-in standard error function, I wrote one. I also wrote a function called "meanse" for presenting the mean, standard deviation, and standard error (rounded to 2 decimal places) of a variable with one call.

```
## FUNCTION FOR COMPUTING STANDARD ERROR:

STDERR <- FUNCTION (X){SD(X)/SQRT(LENGTH(X))}

## FUNCTION FOR COMPUTING MEAN, STANDARD DEVIATION, AND STANDARD
ERROR AT ONCE AND PRESENTING THEM NICELY:

MESNSE <-FUNCTION(X){
      M <- ROUND(MEAN(X),2)
      S <- ROUND(SD(X),2)
      Q <- ROUND(STDERR(X),2)
      R <- C(M,S,Q)
      R <- AS.DATA.FRAME(LIST(MEAN=R[1],SD = R[2],SE=R[3]))
      CLASS(R) <- "TABLE"
      R
}
```

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