ECOLOGICAL HETEROGENEITY: EVALUATING SMALL MAMMAL COMMUNITIES, SOIL SURFACE TEMPERATURE AND ARTIFICIAL NEST SUCCESS WITHIN GRASSLAND ECOSYSTEMS

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for the Degree of
DOCTOR OF PHILOSOPHY
May, 2004

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ACKNOWLEDGMENTS

I am extremely grateful to all who assisted with this extensive project. My dissertation would not be as comprehensive without the assistance of many friends and colleagues. First, I would like to extend my gratitude to Dr. Samuel D. Fuhlendorf for enabling me to grow as a scientist through his guidance and drive for excellence. Additionally, I would like to extend my gratitude to my committe members Dr. David Engle, Dr. David Leslie, Jr., and Dr. Terrance Bidwell for their guidance and instruction throughout my early career as a scientist.

Special thanks to Jay Kerby, Aaron Roper, and Wade Harrell for all the good times, and harassment that I endured on their behalf. I would like to thank Jana Feken for her support throughout the final two years of this study. Finally, I would like to thank my parents, Linda and Darrell Townsend, for stressing the importance of responsibility and commitment and their never-ending support throughout my graduate career.

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CHAPTER 1

ROLE OF ECOLOGICAL HETEROGENEITY FOR CONSERVATION OF SMALL-MAMMAL COMMUNITIES IN TALLGRASS PRAIRIE ECOSYSTEMS

Abstract: Because small mammals are typically the most numerous group of mammals throughout the native prairie ecosystems of the central and northern Great Plains, they serve as an excellent model to study the influence of ecological heterogeneity on conservation of grassland ecosystems. I reasoned that an evaluation of small-mammal communities, could indicate the relative contribution of heterogeneity to conservation and preservation of biodiversity. Our primary objective was to evaluate the influence of the grazing-fire model on vegetation patterns and to determine relationships between heterogeneity and small mammal communities. I hypothesized that a grazing-fire model would produce as shifting mosaic pattern of vegetation composition that would increase heterogeneity beyond the inherent levels associated with traditional approaches to land management and ultimately enhance biodiversity.

Cover of vegetation and heterogeneity differed between treatments. Cover of leaf litter was greater on traditional (i.e. areas that were associated with a fire-return interval ≥ 60 months that represented standard land management for the region) than on patch burn treatments. Alternatively, bare ground was greatest on patch-burn treatments. Patches (within the patch-burn treatments) that were recently burned (< 6 months) were associated with relatively low litter accumulation and high bare ground when compared with patches in the traditional treatments. Forb cover had a positive response to fire and was greater on recently burned patches than on traditional patches. About 36 months following the initiation of patch treatments, cover of bare ground, litter, forbs and tallgrasses begin to reach levels that were similar to traditional treatments. Small-mammal populations were highly influence by cover of bare ground, litter, and forbs.

Patch types that were that were characterized by a fire-return interval ≥ 60 months were associated with high litter accumulation and little bare ground. Species of *Microtus ochrogaster* and *Reithrodontomys fulvescens* numerically dominated these sites within traditional treatments. Species of *Peromyscus maniculatus* and *Chateodipus hispidus* were primarily associated with recently burned patches within the patch-burn treatments. Immediately following a fire event, patch responses were associated with a dramatic shift in site scores along DCA axis-1 and -2. Patch-level vegetation heterogeneity associated with patch-burn treatments was 2.5- to 10-fold greater within patch-burn treatments than on traditional treatments, supporting our initial hypothesis. Patch-burn patches (associated with 25–36 months since focal disturbance) maximized species diversity of small mammals, lending further support for my initial hypothesis.

Key words: *community structure; competition; distribution; habitat selection; landscape; patch; prairie; succession; variability*

INTRODUCTION

Grasslands ecosystems evolved with spatially controlled grazing-fire interactions composed of periodic large- and small-scale disturbances that were highly variable in space and time (Collins and Glenn 1997, Frank et al. 1998, Kaufman et al. 1988, Knapp et al. 1999). The frequency and intensity of grazing and fire are critical to ecological processes, biological diversity, and heterogeneity across multiple spatial scales (Collins 1992, Fuhlendorf and Smeins 1999, Fuhlendorf and Engle 2003). Historically, structure of grasslands were driven by complex interactions between local weather patterns, large ungulate grazing and variable fire return intervals that often determined the intensity of periodic fire disturbances (Weins 1997). These disturbances dictated historical levels of heterogeneity at a variety of spatial and temporal scales (Fuhlendorf and Engle 2001, Fuhlendorf and Engle 2003). This concept of ecological heterogeneity or patchiness has long been recognized by ecologists, but because of its complexity to field studies, heterogeneity was considered to be a statistical challenge that was often 'averaged out' (Keddy 1991).

Scientists adopted an equilibrium paradigm that rarely considered spatial or temporal variability and acted to simplify field studies that resulted in a simplified understanding of ecosystems (Levin 1992, Wiens 1997, Fuhlendorf and Engle 2001, Briske et al. 2003). Scientists acknowledge that historical patterns of variability may have been critical to maintain biological diversity (MacArthur and Pianka 1966, Wiens 1976, Turner and Gardner 1990, Sarnelle et al 1993, Christensen 1997). In fact, heterogeneity may act to stabilize ecological systems by influencing predator-prey or parasite-host interactions, minimizing the spread of disturbances, pests, or pathogens, thereby stabilizing population dynamics and enhancing species diversity (Taylor 1991, Hassell et al. 1993, Huston 1994, Rosenzweig 1995). Recognition of the importance of historical patterns of spatial and temporal variability to biodiversity indicates that conservation and restoration ecology should not be limited to species composition but also should examine spatial and temporal patterns of variability (Fuhlendorf et al. 2002). Because heterogeneity actually may be the root of biological diversity at all levels of ecological organization, it could serve as the foundation for ecosystem conservation and management (Christensen 1997, Ostfeld et al. 1997, Wiens 1997).

Despite the widely recognized influence of ecological heterogeneity on historical ecosystems, most approaches to managing native ecosystems do not consider heterogeneity. Scientists are beginning to acknowledge that disturbance frequencies and patterns associated with many of today's ecosystems have been simplified dramatically from levels that historically occurred, resulting in relatively homogenous ecosystems in space and time (Wiens 1984, Ellis and Swift 1988, Wu and Loucks 1995). For example, traditional grazing practices on the majority of native grasslands promotes uniform distribution of grazing animals within a year reducing heterogeneity below inherent levels created by environmental variables (i.e. soil type, moisture, topography etc.; Fuhlendorf and Engle 2003). The recent loss of such complex disturbance regimes that were associated with historical ecosystems (created primarily by the concept of equilibrium; Briske et al. 2003) is a contributing factor to the loss of biodiversity (Huston 1994, Christensen 1997, Ostfeld et al. 1997, Weins 1997, Fuhlendorf and Engle 2003).

Because recognition of the importance of spatial heterogeneity to biodiversity and conservation has gained recent attention (Levin 1992, Wiens 1997, White and Walker 1997, Sanderson and Harris 2000, Fuhlendorf and Engle 2001, Briske et al. 2003), we developed a heterogeneity model that was designed to establish distinct, spatially discrete vegetation patterns that continually shift within the landscape through space and time (Fuhlendorf and Engle 2001, 2004). According to the model, which is based on pre-settlement disturbance regimes, probability of fire is greatest on areas with high biomass accumulation within a grazed grassland landscape. A positive feedback occurs when a recent fire event attracts grazing animals and their grazing further disturbs the site. A negative feedback occurs when focal disturbance of grazing and fire reduces, biomass, and therefore reduces probability and intensity of fire, which in turn lowers the probability that the patch would be subsequently grazed. Thus, grazing continually shifts through space and time as large herbivores concentrate on patches that recently have been burned, allowing succession on previously burned patches (Fuhlendorf and Engle 2001, 2004). We acknowledge that our model simplifies evolutionary patterns of disturbance, but we propose that restoration of this grazing-fire interaction results in vegetation patterns that more closely resembles historical patterns of heterogeneity than more uniform models associated with the equilibrium paradigm.

These disturbance patterns can have profound influences on wildlife population dynamics (Wiens 1976) and animal movements (Forman and Godron 1986, Gustafson and Gardner 1996). Because spatially discrete disturbance patterns historically have led to a shifting mosaic (Hobbs et al. 1991, Kay 1998, Fuhlendorf and Engle 2001), we presumed that our model will produce alternative habitat types that likely provide 1) complementary resources (i.e., food availability, cover from predators, protection from temperature extremes) capable of improving habitat quality for some species and/or 2) provide unique habitat types capable of supporting a variety of species, both of which could enhance biodiversity.

The overall goal was to evaluate a heterogeneity-based model for conservation and management of grassland ecosystems. Because small mammals are typically the most numerous species of mammal throughout the native prairie ecosystems of the central and northern Great Plains (Grant and Birney 1979, Rose and Birney 1985), they serve as an excellent model to study the influence of heterogeneity on conservation of vertebrates native to grassland ecosystems. Our first objective was to evaluate changes in vegetation cover, litter, bare ground, and vegetation heterogeneity between traditional land management that promotes uniform, moderate disturbances across the landscape and an alternative approach that promotes spatial variability driven by the fire-grazing interaction. The grazing-fire model has previously demonstrated (Fuhlendorf and Engle 2001, Fuhlendorf and Engle 2004) that it can produce a shifting mosaic pattern of vegetation structure that increases landscape heterogeneity. Thus, we hypothesized that species of small mammals would differentially prefer habitats associated with the shifting mosaic. If small mammals are able to respond to the shifting mosaic caused by the fire-grazing interaction, then the increased variability in vegetation structure associated with the shifting mosaic should result in greater diversity or variability within the alternative, heterogeneity-based management approach.

MATERIALS AND METHODS

Study area.–Research was conducted on the1400 ha Oklahoma State University Range Research (OSURR) located about 21 km southwest of Stillwater, Oklahoma. Most of this area is classified as tallgrass prairie in a high seral stage, but some local communities are representative of oak woodlands dominated by *Quercus stellata, Q. marilandica*, and *Juniperus virginiana*. Dominant grasses included *Schizachyrium scoparium*, *Andropogon gerardii* and *Sorghastrum nutans*. Secondary grasses included *Panicum virgatum*, *Sporobolus asper*, *Bouteloua curtipendula* and *Dicanthelium oligosanthes*. The dominant forbs were *Ambrosia psilostachya* and *Gutierrezia dracunculoides*. Taxonomic nomenclature follows Hatch et al. 1990.

To address our primary objective and to determine relationships between heterogeneity and small-mammal communities within tallgrass prairies of the central Great Plains, we used a completely randomized design that included 3 replications of 2 treatments (Patch Burn and Traditional Treatments) on the OSURR. Experimental units (i.e. pastures) ranged in area from 50−60 ha and were divided into 6 equal patches (ca. 8−10 ha) that were delineated at the corners by permanent markers (metal t-posts) designed to facilitate ecological monitoring but not to interfere with livestock or wildlife behavior and distribution. Patches associated with patch burn-treatments were established by applying prescribed fires in spring and summer to 1/6th of the pasture seasonally that resulted in a 3-year fire return interval (Fig. 1a). The objective of this management approach was to have 6 patches that vary in vegetation structure with time since fire and season of fire. The traditional treatments were not burned during our study and were associated with a fire-return interval ≥ 60 months that represented standard land management for the region. Experimental units of both traditional and patch-burn treatments were moderately grazed by free-ranging stocker cattle ($\bar{x} = 270$ kg) at about 3 ha/animal from 1 December to 31 September. Treatments were treated similarly except for the application of spatially discrete fires in the patch-burn treatment, where grazing animals were allowed to select recently burned patches so that interactions between fire and grazing could be considered simultaneously.

Vegetation sampling. – Detailed analyses of vegetation composition and structure have been documented previously on our study site (Fuhlendorf and Engle 2004). I report results useful in evaluating the hypothesis that small mammals respond to the shifting mosaic pattern of vegetation structure and composition. Vegetation composition was sampled from late August to early September in 2001 and 2002. For each patch within each treatment, I recorded canopy cover of plant functional groups (forbs, *S. scoparium*, tallgrass, other grasses and total grass) leaf litter and bare ground by cover classes within 30, 20 x 50-cm randomly located quadrats (Fuhlendorf and Engle 2004), so that differences in vegetation communities between treatments could be detected. We calculated the mean standard deviation among patches within each treatment as an index of heterogeneity so that levels of heterogeneity could be assessed between traditional and patch-burn treatments.

Small-mammal sampling. – Species of small mammals were censussed about every 2.5 months on each patch of each treatment during May – June, August – September, November – December of 2001 and March – April, July – August, and October – November of 2002. One sampling period covered a span of 18 days. Thus, to prevent any biases associated with changes in weather patterns (i.e. temperature or rainfall that are likely to influence trap success) throughout an 18-day sampling period, patch burn and traditional patches were censussed simultaneously. For instance, replicated patch pairs were established (i.e. treatment patch # 1 – 6 corresponded to a traditional patch # 1 – 6), where experimental units with identical patch numbers constituted 1 patch pair per replication (i.e. patch pair # 1 = treatment patch #1 + traditional patch # 1 for each of 3 replications; Fig. 1b). Trapping occasions were subdivided so that one patch pair was sampled concurrently. Replicated patch pairs were selected randomly (RANUNI, SAS Institute, Inc. 2000) and censussed using 2 40 x 40 m grids per patch that were placed randomly in tallgrass prairie habitat (5 x 5 trapping grid with 10-m spacing). Each grid contained 25 traps and one trapping occasion was restricted to one patch pair per replication (i.e. 100 traps/patch pair per replication or 300 traps). Each sampling period required 6 trapping occasions (i.e. 6 patch pairs/replication) where each trapping occasion was sampled for 3 consecutive nights (i.e. 1 sampling period requires 18 trap nights; Fig. 1b).

Mammals were trapped with Sherman live-traps (7.6 x 8.9 x 22.9 cm) baited with rolled oats and supplied with cotton for bedding during fall and winter trap sessions. Upon capture, each animal was identified to species; sex and age (adult or juvenile) were determined; and each individual was marked by toe-clipping and with a numbered aluminum ear tag (National Band and Tag Co., Lexington, KY). Rodent trapping conformed to guidelines sanctioned by the American Society of Mammalogists (Animal Care and Use Committee 1998). Relative abundance was computed as the number of animals caught per 100 trap-nights. A trap-night was defined as one functional trap open for a 24-h period (McMurry et al. 1994). To account for variation in sprung traps among sites, traps found sprung and empty were subtracted from analyses.

Statistical analysis.– Analysis of variance (PROC ANOVA, SAS Institute Inc. 2000) was used to evaluate the significance of changes in vegetation cover, bare ground and heterogeneity between treatments. As an index of heterogeneity we used analysis of variance (PROC ANOVA, SAS Institute, Inc. 2000) to test the null hypotheses that there are no differences in the mean standard deviation between each treatment (i.e. we calculated the mean standard deviation between 6 patches associated with each treatment). These tests assessed differences between treatments and served to address our hypothesis that the grazing-fire model associated with patch burning increased heterogeneity beyond levels associated with traditional treatments. Vegetation change in the patch-burn treatments was anticipated to have a strong relationship with time since fire because of subsequent structural and compositional changes associated with the grazing-fire interaction. Thus, vegetation response to time since fire was correlated with vegetation cover, bare ground and litter cover, to determine the relative influence of fire on patterns of vegetation. Those relationships were computed to further address our first hypothesis and to determine if spatially discrete fires contribute to a shifting mosaic vegetation pattern across the landscape. We calculated mean and standard errors to address our second hypothesis that species of small mammals would differentially prefer patches associated with different habitat types. We tested the null hypotheses that there are no differences in pooled capture rates (captures/100 trap nights) among treatments, where overlapping standard errors were deemed not significant. We calculated the mean species diversity index H' using the logarithmic base 10 (Shannon and Weaver 1949). Species diversity was calculated from relative abundance values that were derived from the mean number of individuals captured/100 trap nights to allow for direct comparisons between traditional treatments and patch-burn patches. Overlapping standard error bars were compared to assess differences in species diversity between patch type and treatment.

We used a detrended correspondence analysis (DCA) to describe differences among trap sites based on abundance of small mammal communities using PCORD for Windows (McCune and Mefford, 1999). DCA provides a mechanism to summarize general patterns of similarities and differences among samples and has been used to quantify dynamics in communities over time (Collins 2000). That technique was used to determine influences of patch type on small-mammal communities within tall grass prairies of the central Great Plains and further addressed our second goal of evaluating relationships between our grazing-fire model and small-mammal communities. Due to extremely low capture rates in May−December 2001 (presumably associated with winter storms in December and January of 2000 and 2001), all DCA analyses were based on data collected during March−November 2002, where capture rate was ≥ 5 captures/100 trap nights (Fig. 2). We used the Dufrene and Legendre's (1997) method of calculating species indicator values using PCORD for Windows (McCune and Mefford 1999) to determine if abundance of small mammal species could be used as another indicator of habitat preference. Significance of these tests were determined using a Monte Carlo permutation technique with 1000 iterations and were deemed significant when $P \leq 0.05$. Taken together (i.e. DCA and species indicator values), these analyses were intended to address habitat preferences associated with our second hypothesis that species of small mammals differentially preferred patch types. After the ordination, we used an analysis of variance (PROC ANOVA, SAS Institute Inc. 2000) to test the null hypotheses that there are no differences in DCA axis scores among treatments, so that differences in small-mammal abundance could be further evaluated. Although DCA site scores are not truly independent, the ANOVA is used as an aid to interpret axes rather than interpret the diagram as a whole (Collins 2000, ter Braak 1995). To further address our second goal and to determine if small mammals responded to a shifting mosaic associated with our grazing-fire model, we used a regression analysis to determine the influence of time since fire on DCA axis-1 and axis-2 scores. We tested the suitability of our regression model using a Hosmer-Lemeshow test for goodness-of-fit (Hosmer and Lemeshow 1989:140) where $P > 0.05$ indicated the model fit. A significance level of $\alpha < 0.05$ was set for all appropriate tests.

RESULTS

Heterogeneity and Patterns of Vegetation

Vegetation cover and heterogeneity among patches differed between treatments. Cover of litter and other grasses were greatest on traditional treatments while forb cover and bare ground was greatest on patch burn sites (Table 1). Bare ground and forb cover was correlated negatively with the number of months since fire, while litter and tallgrasses were correlated positively with months since fire (Fig. 2). Heterogeneity of bare ground (standard deviation between patches) was 10 times greater, while heterogeneity of litter and forb cover was nearly 3 times greater on patch burn treatments than in traditional treatments. Heterogeneity of other perennial grasses was > 2.5 times greater on patch-burn treatments than traditional treatments (Table 1). Analysis of heterogeneity of those functional groups indicated that the patch-burn treatment increased heterogeneity of vegetation at the scale of patches.

Patch-burn patches that were recently burned (< 6 months) were associated with relatively low litter accumulation and high bare ground compared with patches within the traditional treatments (Fig. 2). Forb cover was greatest on patch-burn patches associated with 12 months since fire and generally decreased with time thereafter (Fig. 2). About 36 months following the initiation of patch treatments, cover of bare ground, litter, forbs and tallgrasses begin to reach levels that were similar to traditional treatments (Fig. 2). Cover of *S. scoparium* and total grasses were similar to traditional treatments approximately 11−23 and 23−25 months following a fire event, respectively (Fig. 2), suggesting that our grazing-fire model produced a shifting mosaic pattern that incorporated a wide range of vegetation patterns, including patches of habitat similar in composition to traditional patches and patches with reduced litter and tallgrasses but increased bare ground and forbs (See Fuhlendorf and Engle 2004 for details).

Patch Dynamics and the Small Mammal Community

We captured 7 species (1,399 individuals) of small mammals. Two species (*Peromyscus leucopus*, n = 6; *Reithrodontomys montanus*, n = 8), representing 1% of individuals captured, were collected incidentally and were excluded from analyses. As a result, our analyses were based on 1,385 individuals and 5 species. There were differences in capture rate (i.e. # of individual captures / 100 trap nights) among the five species of small-mammals throughout our study period. Overall capture rate was greatest in small-mammal communities from traditional treatments than from patch burn treatments in trapping session 3, 4, and 5 (November 2001 – August 2002), but by the end of our study (trap session 6), treatments did not differ (see species pooled; Fig. 3). There were no differences between the remaining 3 trapping sessions. Capture rate for *Peromyscus maniculatus* ($\bar{x}$ = 0.46/100 trap nights) and *Microtus ochrogaster* ($\bar{x}$ = 0.43/100 trap nights) were higher than for all other species. Capture rates for *Sigmodon hispidus* ($\bar{x}$ = 0.26/100 trap nights) and *Reithrodontomys fulvescens* ($\bar{x}$ = 0.22/100 trap nights) were higher than *Chateodipus hispidus* ($\bar{x}$ = 0.05/100 trap nights, $P \leq 0.05$).

Relative abundance of small mammals were influenced by the application of the grazing-fire model. The first two DCA axes based on the abundance of small mammals explained 79.7% of the variance in site and species scores (axis-1 eigenvalue = 0.547; axis-2 eigenvalue = 0.250; Fig. 4). Multiple regression analysis of DCA axes with time since fire accounted for 68% of the total variation in DCA axis-1 and 36% in axis-2 scores ($P < 0.001$, Fig. 5), indicating that most of the variation in axis-1 and -2 scores on patch-burn treatments was explained primarily by time (months) since fire (Fig. 4). The standard deviation of DCA axis-1 scores did not differ between treatments, but the standard deviation associated with DCA axis-2 scores were consistently greater within the patch-burn treatments (Fig. 6), providing additional indication that patch-burn treatments were more heterogenous.

Mean DCA axis-1 scores on traditional sites ($\bar{x} = 105 \pm 7.75$) were lowest than on patch burn sites ($\bar{x} = 216 \pm 7.74$; $P < 0.001$) and mean DCA axis-2 scores were highest on traditional sites ($\bar{x} = 80 \pm 4.15$) than on patch-burn sites ($\bar{x} = 54 \pm 7.90$; $P = 0.004$), indicating treatment differences. Low DCA axis-1 and high axis-2 scores were associated with a greater abundance of *M ochrogaster*, *R. fulvescens*, and *S. hispidus* (Fig. 4). Alternatively, high DCA axis-1 and low DCA axis-2 scores were associated with a greater abundance of *P. maniculatus*. *C. hispidus* was associated with high DCA axis-1 and -2 scores (Fig. 4).

Abundance of small mammals responded to time since fire. For instance, patch-burn patches responded to fire along DCA axis-1 and axis-2 through time, where the most recently burned patches started their trajectory through time at high DCA axis-1 and low DCA axis-2 scores. As time since fire increased, the trajectory path on DCA axes moved up and to the left (i.e. DCA axis-1 decreased and the trajectory path on DCA axis-2 tended to increase; Fig 4), resulting in a shifting mosaic of patch types that included sites that had been recently burned and grazed, sites that were in various stages of recovery, and sites that had not been disturbed for ≥ 3 years. Further, DCA axes suggested that small-mammal populations may fully recover to pre-disturbance levels within a 3-year fire return interval (Fig. 4). For instance, within 3 years post fire, patch-burn patches are indistinguishable from traditional patches. Capture rates associated with *P. maniculatus* and *S. hispidus* provided additional indication that patch-burn patches with a fire return interval ≥ 36 months are similar to traditional patches. However, capture rates associated with *M ochrogaster* and *R. fulvescens* associated with patch burn patches with a fire return interval ≥ 36 months suggest that abundances of these 2 species do not fully recover to levels associated with traditional patches (Fig. 7).

Application of the grazing-fire model altered patterns of small-mammal abundance. Cover of litter, forbs, and bare ground accounted for most of the variation in abundance of small mammals. Capture rates of *C. hispidus* were greater in patch burn than in traditional treatments in 5 of 6 trap sessions. Similarly, capture rates of *P. maniculatus* were greater in patch-burn treatments than in traditional treatments (Fig. 3), and species-indicator values provided additional indication that deer mice were associated primarily with patch-burn treatments (Table 2). Abundances of *C. hispidus* and *P. maniculatus* were correlated positively with forbs and bare ground and negatively with leaf litter (Table 3), sites typically found within patch burn patches that were burned ≤ 36 months ago (Fig. 2, 7). Species of *C. hispidus* were essentially non-existent within traditional treatments (Fig. 7). Capture rate of *P. maniculatus* were greater on patches that were burned ≤ 36 months (Fig. 7), suggesting that fire return intervals ≤ 36 months support a greater abundance of *P. maniculatus*.

Habitat preferences of small mammals were influenced by our grazing-fire model and were dynamic through time. Mean capture rate (Fig. 3) and species indicator values (Table 2) suggested that *M. ochrogaster* and *R. fulvescens* were more abundant in traditional treatments. Capture rates for *S. hispidus* were greatest on patches associated with ≥ 36 months since fire and were highly abundant within the patch burn but only in patches associated with with ≥ 36 months since fire (Fig. 7). Capture rates of *M. ochrogaster* and *R. fulvescens* were correlated negatively with bare ground and positively with litter cover (Table 3), sites that were characterized by traditional treatments and patch burn patches with a fire return interval > 36 months (Fig. 2). However, capture rates of *M. ochrogaster* and *R. fulvescens* associated with patch-burn patches with a fire return interval of 25 – 36 months were lower than those associated with traditional treatments (Fig. 3). Capture rates of *S. hispidus* associated with patches that had been burned between 25 and 36 months were similar to capture rates associated with traditional patches (Fig. 3).

Species diversity of small mammals (within the patch burn treatment) increased with time since focal disturbance (grazing-fire interaction), and was greatest in patch-burn patches that were associated with a fire-return interval of 25 – 36 months. Species diversity associated with patches that were ≥ 13 months since fire did not differ but were significantly greater than patches that had been burned within a year (12 months). Species diversity did not differ between traditional and patch-burn treatments (Fig. 7).

DISCUSSION

Implementation of Heterogeneity as a Conservation Tool

A patch work of habitat types was important to the evolutionary history of grasslands in the North American Great Plains. These habitat types likely provided complementary resources (i.e. food availability, cover from predators or protection from extreme temperatures) that improved habitat quality for a variety of species, presumably enhancing biodiversity. Often, current resource management practices (associated with grassland ecosystems) strive to simplify ecosystems by reducing heterogeneity. Much of the inherent heterogeneity associated with native grasslands has been reduced by promoting a uniform distribution of grazing animals across the landscape. A homogeneity-based approach to our natural resources often comes at a significant cost to ecosystem function (Christensen 1997). Ecologists are beginning to recognize that complex heterogenous ecosystems are critical elements to sustain biodiversity and ecosystem function (Tartowski et al. 1997).

Conservation often involves the restoration of damaged or degraded ecosystems and reestablishment of historical plant and animal communities (White and Walker 1997, Stephenson 1999, Kloor 2000). Restoration efforts also should attempt to conserve community composition, protect the patterns of variability critical for biological and environmental diversity, and maintain the processes that produce those patterns of variability (Christensen 1997). Grazing and fire are important ecological processes that contributed to the development of many grassland ecosystems (Knapp et al. 1999, Collins

2000). In the absence of fire, grasslands eventually develop into shrubland and woodland vegetation (Petranka and McPherson 1979). Thus, periodic fire is a necessary and critical ecosystem component that stabilizes native grasslands by enhancing grass production and deterring establishment of woody plants (Gibson and Hulbert 1987, Anderson 1990, Bragg 1995). Patch-burning was developed to restore complexity and heterogeneity to our native grasslands by incorporating the same basic processes (i.e. grazing-fire interactions) that shaped historical grasslands into today's ecosystems. Although application of the heterogeneity-based model simplifies the evolutionary disturbance patterns of historical grasslands, it contributes to more vegetation patterns that presumably more closely resemble historical patterns than do uniformity based approaches to conservation (Fuhlendorf and Engle 2004). This model serves to compare relationships between traditional management practices and an alternative patch-burn system that allows grazing animals to select recently burned patches so that fire and grazing disturbances could be evaluated simultaneously as an effective conservation tool for our remaining grassland ecosystems (Fuhlendorf and Engle 2001, 2004).

Small-mammal Community Response

Small-mammal populations differentially preferred habitats associated with the shifting-mosaic. For instance, small-mammal populations primarily responded to cover of bare ground, litter, and forbs (Table 3). Habitat characteristics associated primarily with exposed soil and limited vertical structure generally support higher abundances of *P. maniculatus* and *C. hispidus* (Kaufman et al. 1983, Schramm and Willcutts 1983, Snyder and Best 1988, Kaufman et al. 1988, Paulson 1988, Clark et al. 1998), while those associated with abundant vegetation cover and a well-developed litter layer supported species of *M. ochrogaster* and *R. fulvescens*. Patch-burn patches supported greater abundances of *P. maniculatus* and were a key requirement for the presence of *C. hispidus*.

Traditional Patches.– The DCA illustrated the influence of the grazing-fire model on species of small mammals. Low axis-1 scores were representative habitats associated with dense vegetation cover and a well-developed layer of senescent litter accumulation. These patch types were associated primarily with all patches within traditional pastures that were characterized by a fire-return interval ≥ 36 months. Species of *M. ochrogaster* and *R. fulvescens* numerically dominated these sites within traditional patches, supporting previous reports of habitat preferences for these species (Kaufman and Fleharty 1974, Spencer and Cameron 1982, Kaufman et al. 1990, Clark et al. 1998). Species of *M. ochrogaster* reached their highest densities on traditional treatments during Nov-Dec '01 and Mar-Apr '02 before declining in the following trap sessions (Jul-Aug '02 and Oct-Nov '02). Habitat selection is known to change with competition and habitat quality (Viitala and Pusenius 1990). Although, vole habitat associated with traditional treatments remained relatively unchanged, subsequent *M. ochrogaster* declines were perhaps in response to significant increases in *S. hispidus* density during Jul-Aug and Oct-Nov '02. Our data supported the conclusions by Fleharty and Olsen (1969) who argued that competition exists for space rather than for food. Thus, it is likely that *S. hispidus*, a behaviorally dominant competitor (Prochaska and Slade 1981), may have limited vole abundance during Jul-Aug and Oct-Nov ‘02. Competition for space likely influenced the negative interactions between *S. hispidus* and *M. ochrogaster*. For instance, *M. ochrogaster* abundance flourished when *S. hispidus* abundance was relatively low during Nov-Dec ‘01 and Mar-Apr ‘02. Conversely, increases in *S. hispidus* abundance during Jul-Aug ‘02 and Oct-Nov ‘02 corresponded with decreased abundance of *M. ochrogaster*. Several studies have documented strong support for such interactions and have documented negative relationships between *S. hispidus* and *M. ochrogaster* (Prochaska and Slade 1981, Foster and Gaines 1991, Diffendorfer et al. 1995, 1996). Further, *M. ochrogaster* and *P. maniculatus* have been found to be strong competitors (Abramsky and Tracy 1979, Stalling 1990). However, despite a 38% diet overlap (Cook et al. 1982, Stalling 1990), *P. maniculatus* did not co-occur with *M. ochrogaster* on our study site (Fig. 4), suggesting that neither species’ niche is included in that of the other.

Patch Burn Patches.–Species of *P. maniculatus* and *C. hispidus* were primarily associated with high axis-1 scores that were shaped primarily by recent fire and subsequent grazing by large herbivores. Immediately following a fire event, patch responses were evident and illustrated by a shift in site scores along DCA axes-1 and -2. For instance, axis-1 scores, move from c.a. ≤ 150 to ≥ 250 and axis-2 scores move from c.a. ≥ 90 to ≤ 10. Species of *P. maniculatus* were most abundant in patch-burn patches associated with a fire-grazing history ≤ 12 months but remained highly abundant in patch-burn patches associated with a grazing-fire history < 36 months. Species of *C. hispidus* were almost exclusively associated with patch-burn patches with a fire return interval ≤ 36 months (Fig. 7). These two species were likely responding to habitat characteristics primarily driven by grazing-fire interactions. For instance, focal fire and subsequent grazing by large herbivores act in concert to reduce tallgrasses and increases herbaceous dicots (Fuhlendorf and Engle 2004). These habitat types generally persist for about 1 – 2 years (Fuhlendorf and Engle 2004) and produce habitat types associated primarily with increased bare ground and highly variable vertical structure, supporting previous reports of habitat preferences for *P. maniculatus* and *C. hispidus* (Kaufman et al. 1983, Schramm and Willcutts 1983, Snyder and Best 1988, Kaufman et al. 1988, Paulson 1988, Clark et al. 1998). Declines in *M. ochrogaster* also were evident in patch-burn treatments in response to significant increases in *S. hispidus* density during Jul-Aug and Oct-Nov '02, further indicating a strong negative interaction between *M. ochrogaster* and *S. hispidus* density (Fig. 2).

As patches begin to recover, temporal changes associated with seral stage of recovery following a focal disturbance (i.e. grazing-fire interaction) become quite evident. Scores on DCA axes progressively move up and to the left corresponding with successional changes in vegetation driven by periodic fire disturbances (i.e. DCA axis-1 scores progressively decrease as scores on DCA axis-2 progressively increase). Ultimately, patches within patch burn pastures become indistinguishable from control patches (patch burn patch # 2 is indistinguishable from traditional patches during Oct-Nov '02; Fig. 4), resulting in a heterogenous landscape composed of sites that have been recently burned and grazed, sites that were in various stages of successional recovery, and sites that had not been disturbed for about 3 years (Fig. 4). Over time these patches ultimately produce a mosaic of patch types in various successional phase transitions that are preferred by several species of small mammals. Species of *P. maniculatus* numerically dominated patches that were associated with grazing-fire focal patch disturbances ≤ 12 months. This patch type proved to be the least diverse of all patch types but was dominated by 2 primary species (*C. hispidus*, *P. maniculatus*). Abundance of *M. ochrogaster* and *R. fulvescens* increased with time since fire and focal grazing, which was most likely in response to increases in vegetation cover and litter accumulation followed by subsequent decreases in bare ground. Thus, depending on time since fire, patch-burn treatments produce a variety of patch (habitat) types ranging from relatively undisturbed patch types (that are similar in vegetation composition to traditional patches; i.e. high litter accumulation and relatively little bare ground) to patch types that are highly disturbed and focally grazed (i.e. high bare ground and low litter accumulation).

CONCLUSIONS

Application of our grazing-fire model contributed to ecological heterogeneity and enhanced biodiversity of vegetation cover and small-mammals. Patch-level heterogeneity associated with patch burn treatments was 2.5- to 10-fold greater within patch burn treatments than on traditional treatments, supporting our initial hypothesis. The heterogeneity model implements a fire regime that acts to shift grazing disturbances to more recently burned areas, where patches associated with a fire-return interval ≥ 3 years are dominated again by tallgrasses and high litter accumulation (Fuhlendorf and Engle 2004).

This pattern forms a shifting mosaic of out of phase successional stages (driven by time since focal disturbance) that produced habitat conducive for nearly all small mammal species found on our study sites. The grazing-fire model supports the notion that heterogenous systems are capable of enhancing biodiversity. For instance, species diversity (within the patch burn treatment) increased with time since focal disturbance (grazing-fire interaction) and was greatest in patches that were associated with a fire-return interval between 25 and 36 months. Although grazing-fire focal disturbances associated with 0 to 12 months was the least diverse patch, species of *C. hispidus* are dependant on the habitat types created by this disturbance pattern.

Spatial and temporal patterns of vegetation variability contribute to landscape patchiness and have been suggested to be as important as composition (Wiens 1997, Christensen 1997). Thus, incorporation of multiple patch structure to increase ecological heterogeneity may be critical to conservation ecology and biodiversity. It is clear that management techniques designed to restore historical levels of heterogeneity can have a dramatic influence on the distribution and abundance of small-mammal communities. Our study demonstrates that the grazing-fire model serves as an alternative to traditional management practices. Patch fires and large herbivore grazing can be useful conservation tools for many grassland ecosystems because when used simultaneously they can increase heterogeneity and maximize biodiversity by producing a shifting mosaic of habitat types through space and time.

Fire is perhaps the most important ecosystem component maintaining native grasslands. In the absence of fire, grassland communities may experience a rapid increase in woody vegetation cover by as much as 1% per year (Bragg and Hulbert 1976, Collins and Gibson 1990), eventually converting native prairies into shrublands or woody communities dominated by eastern redcedar (*Juniperus virginiana*). On our study site, species of *C. hispidus* are essentially non-existent on patches where fire has been suppressed (i.e. ≥ 60 months). Although the patch-burn model tended to decrease the relative abundance of some species (i.e. *M. ochrogaster* and *R. fulvescens*), it did not have a significant impact on reducing species diversity. In fact, species diversity was greatest within patch-burn patches associated with a grazing-fire history between 25 and 36 months.

Given the current status of the Great Plains grasslands, recovery or conservation of historical patterns of landscape variability and heterogeneity is highly unlikely, primarily because of the vast spatial scales at which they occurred. Analysis of multiple scales are necessary to accurately describe relationships between organisms and their environment (Fuhlendorf and Smeins 1996, 1998). Thus, caution should be used when interpreting the significance of patch-burn management techniques to species of small mammals without considering spatial scale at which these processes are observed. However, re-creating a shifting mosaic of vegetation patterns that is dispersed across the landscape may more closely resemble the evolutionary forces that shaped modern native grasslands than more homogenous based systems that are currently implemented throughout the northern Great

Plains. Because, historical disturbance patterns, presumably provided habitat types that maximized biodiversity, attempting to re-create patterns of spatial and temporal variability at any scale may be a critical component in conservation ecology.

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Table 1. Vegetation cover and degree of landscape heterogeneity in control and patch burn pastures on the Oklahoma State University Range Research Station, Stillwater, Oklahoma. Mean standard deviation between six patches associated with each treatments was used as an index to heterogeneity.

Vegetation cover type	Traditional			Patch Burn				
	n	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*F*	*P*
Percent cover								
Bare ground	3	2	0.91	3	25	4.17	28.72	0.006
Leaf litter	3	70	3.42	3	45	2.67	34.86	0.004
Forb	3	11	0.36	3	20	1.15	47.02	0.002
S. scoparium	3	12	1.65	3	12	0.84	0.11	0.756
Tallgrass	3	17	10.11	3	17	2.99	0.00	0.996
Other grasses	3	19	1.88	3	25	0.72	10.49	0.032
Total grass	3	58	2.46	3	54	2.91	1.00	0.374
Index of Heterogeneity								
Bare ground	3	2	0.74	3	15	0.80	156.2	0.001
Leaf litter	3	5	1.20	3	14	1.79	17.05	0.015
Forb	3	3	0.41	3	5	1.40	2.25	0.208
S. scoparium	3	2	0.19	3	1	0.25	2.67	0.178
Tallgrass	3	7	1.06	3	9	0.89	1.71	0.261
Other grasses	3	4	0.52	3	6	0.39	15.73	0.017
Total grass	3	2	0.60	3	5	0.59	13.74	0.021

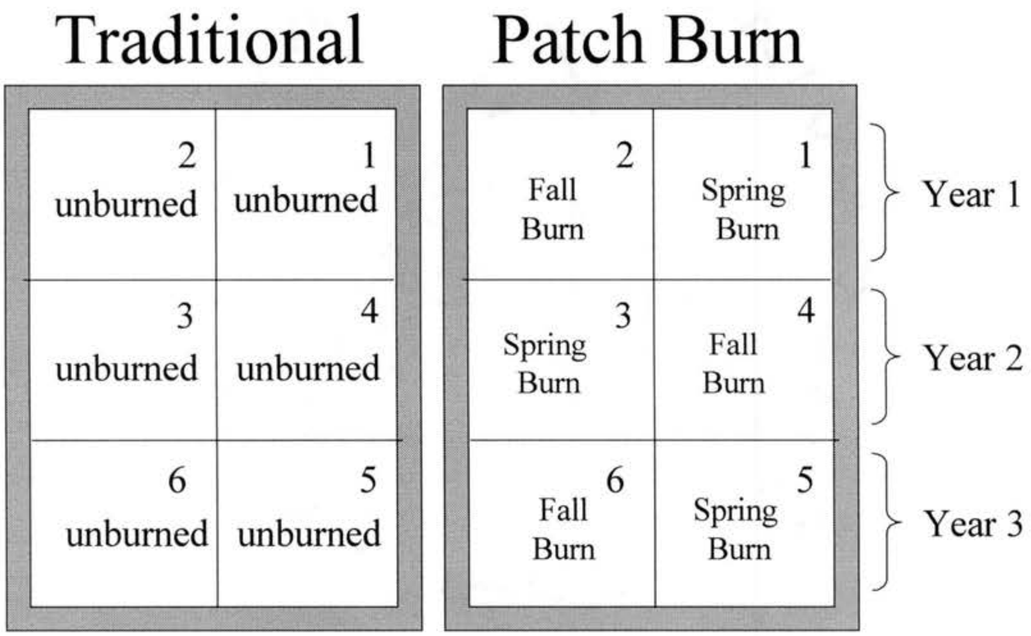
Table 2. Species indicator values (Dufrene and Legendre 1997) of ecological disturbance for control (homogenous, low disturbance) and patch burn (heterogenous, high disturbance created by the grazing-fire model) treatments for five species of small mammals on the Oklahoma State University Range Research Station, Stillwater, Oklahoma, 2002.

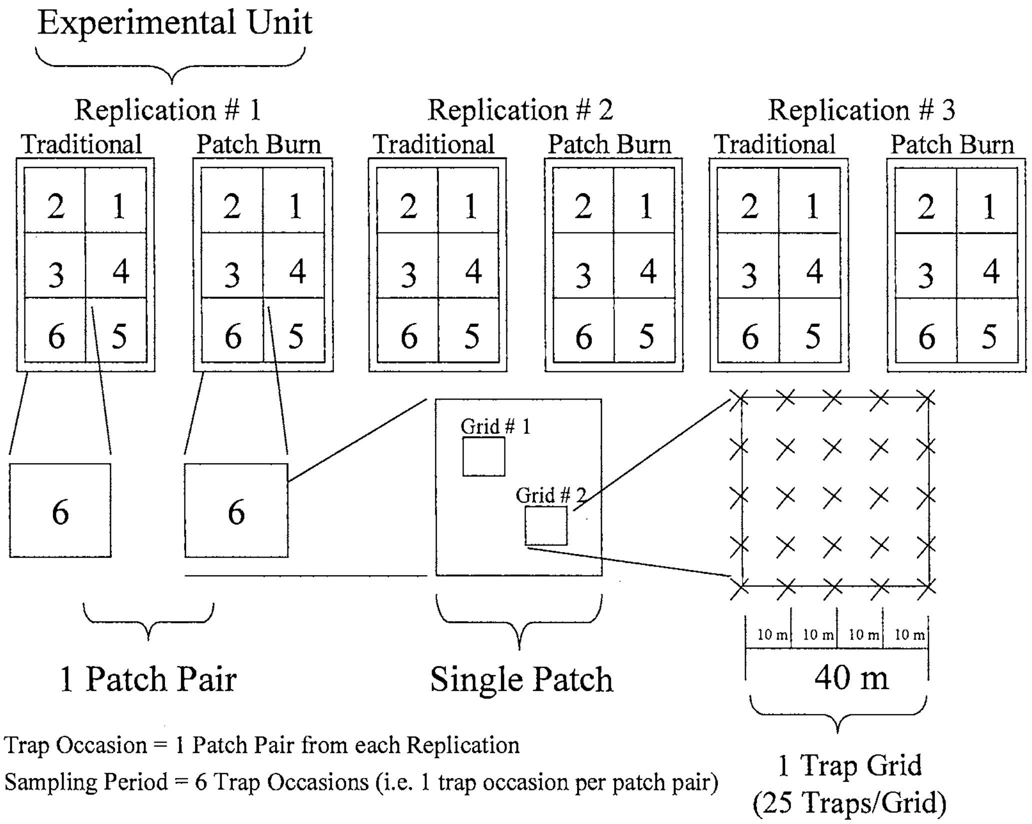
	Indicator Value (IV)		IV from randomized groups		
Species	Traditional	Patch Burn	$\bar{x}$	*S.D.*	*P*
C. hispidus	0	29	12.8	3.0	<0.001
P. maniculatus	24	62	45.6	3.7	0.001
M. ochrogaster	72	1	28.7	3.9	<0.001
R. fulvescens	72	4	32.8	4.1	<0.001
S. hispidus	51	11	32.1	4.1	0.001

Table 3. Correlation coefficients for the relationships between vegetation cover and small mammal abundance on the Oklahoma State University Range Research Station, Stillwater, Oklahoma 2002.

	C. his.		*P. man.*		*M. och.*		*R. ful.*		*S. his.*	
	r	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Bare ground	0.38	0.024	0.31	0.070	-0.55	<0.001	-0.49	0.003	-0.44	0.008
Leaf litter	-0.43	0.009	-0.39	0.018	0.65	<0.001	0.51	0.001	0.40	0.016
Forb	0.52	0.001	0.35	0.037	-0.52	0.001	-0.52	0.001	-0.25	0.136
S. scoparium	-0.15	0.392	0.17	0.315	-0.07	0.704	0.16	0.342	-0.06	0.726
Tallgrass	-0.09	0.596	-0.34	0.044	0.57	<0.001	0.13	0.467	0.23	0.172
Total grass	-0.05	0.770	-0.18	0.283	0.30	0.074	0.06	0.714	0.120	0.485

Figure 1. Schematic of the experimental design of 3 replicated treatments (traditional, patch burn) and a graphic illustration identifying locations of trapping grids on the Oklahoma State University Research Range, Stillwater, Oklahoma. The bold outer rectangles represent pasture boundaries (≈ 60 ha), while the inner rectangles represent the boundaries of 6 equal patches (≈ 10 ha). (a) Patches associated with patch burn treatments were established by 1) prescribing spring and fall fires to 1/3 rd of the pasture annually, resulting in a 3-year fire return interval. Patches within traditional treatments were associated with a fire return interval ≥ 60 months and remained unburned throughout our study. (b) Replicated patch pairs were established, where experimental units with identical patch numbers constituted 1 patch pair per replication. Trapping occasions were subdivided so that one patch pair was sampled concurrently and censussed using 2 40 x 40 m grids per patch that were randomly placed in tallgrass prairie habitat (5 x 5 trapping grid with 10-m spacing). Each grid contained 25 traps and one trapping occasion was restricted to one patch pair per replication (i.e. 100 traps/patch pair per replication or 300 traps across all replications). Each sampling period required 6 trapping occasions (i.e. 6 patch pairs/replication) where each trapping occasion was sampled for 3 consecutive nights.


Traditional
Patch Burn
2 unburned
1 unburned
3 unburned
4 unburned
6 unburned
5 unburned
2 Fall Burn
1 Spring Burn
3 Spring Burn
4 Fall Burn
6 Fall Burn
5 Spring Burn
Year 1
Year 2
Year 3



1 Trap Occasion = 1 Patch Pair from each Replication

1 Sampling Period = 6 Trap Occasions (i.e. 1 trap occasion per patch pair)

Figure 2. Relationships between ground cover and time (months) since fire on the Oklahoma State University Research Range, Stillwater, Oklahoma, 2002. Each scatterplot represents values associated with patch burn patches. Mean and standard error bars represent mean cover values for traditional treatments associated with a fire return interval ≥ 60 months.

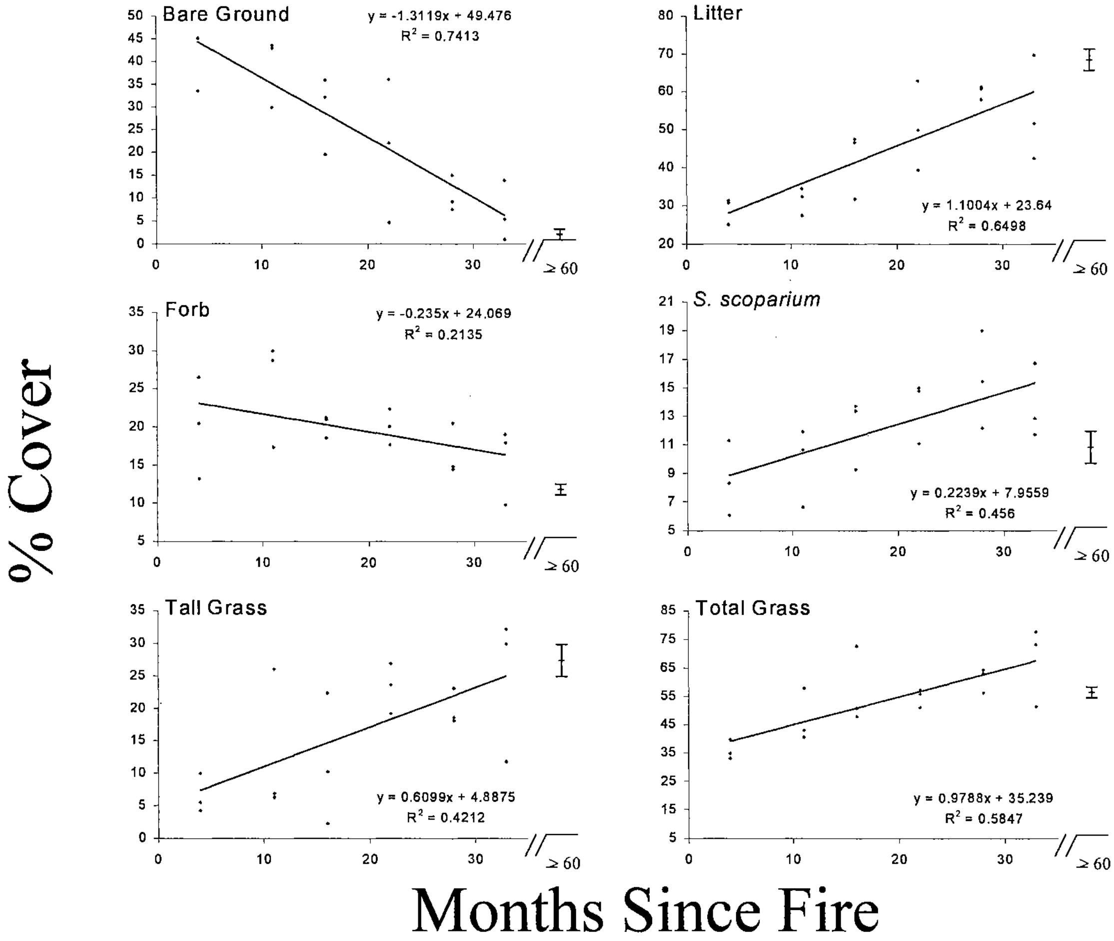

% Cover
Months Since Fire
Bare Ground
y = -1.3119x + 49.476
R² = 0.7413
50
45
40
35
30
25
20
15
10
5
0
0
10
20
30
≥ 60
Litter
y = 1.1004x + 23.64
R² = 0.6498
80
70
60
50
40
30
20
0
10
20
30
≥ 60
Forb
y = -0.235x + 24.069
R² = 0.2135
35
30
25
20
15
10
5
0
10
20
30
≥ 60
S. scoparium
y = 0.2239x + 7.9559
R² = 0.456
21
19
17
15
13
11
9
7
5
0
10
20
30
≥ 60
Tall Grass
y = 0.6099x + 4.8875
R² = 0.4212
35
30
25
20
15
10
5
0
0
10
20
30
≥ 60
Total Grass
y = 0.9788x + 35.239
R² = 0.5847
85
75
65
55
45
35
25
15
5
0
10
20
30
≥ 60

Figure 3. Abundance (mean individual captures/100 trap nights) of 5 small mammal species on control ($n = 3$) and patch burn ($n = 3$) treatments. Numbers above bars represent total number of captures/100 trap nights within a given trap session.

Traditional ☐ Patch Burn ▨

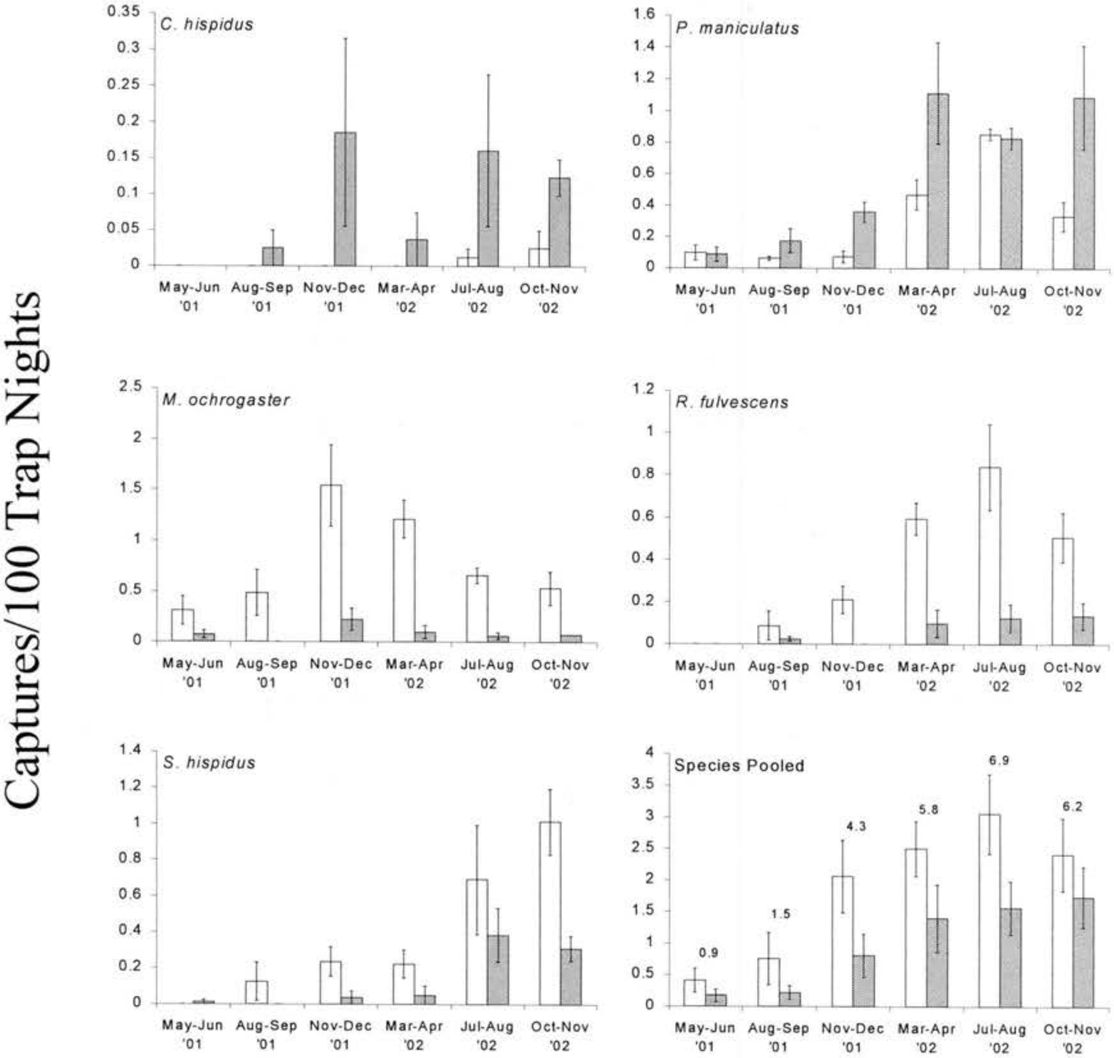

Captures/100 Trap Nights
C. hispidus
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
P. maniculatus
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
M. ochrogaster
2.5
2
1.5
1
0.5
0
R. fulvescens
1.2
1
0.8
0.6
0.4
0.2
0
S. hispidus
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Species Pooled
4
3.5
3
2.5
2
1.5
1
0.5
0
0.9
1.5
4.3
5.8
6.9
6.2
May-Jun '01
Aug-Sep '01
Nov-Dec '01
Mar-Apr '02
Jul-Aug '02
Oct-Nov '02

Figure 4. Detrended Correspondence Analysis (DCA) of the abundance of 5 small mammal species from traditional and patch burn treatments throughout 3 trap sessions (March-April, July-August, and October-November) during 2002. (a-c) Solid envelope encompasses site scores for traditional treatment and dashed envelopes encompasses sites scores for patch burn treatment, (d) DCA axes associated with species scores illustrated at larger axes scales to include the relative position of 5 primary small mammal species.

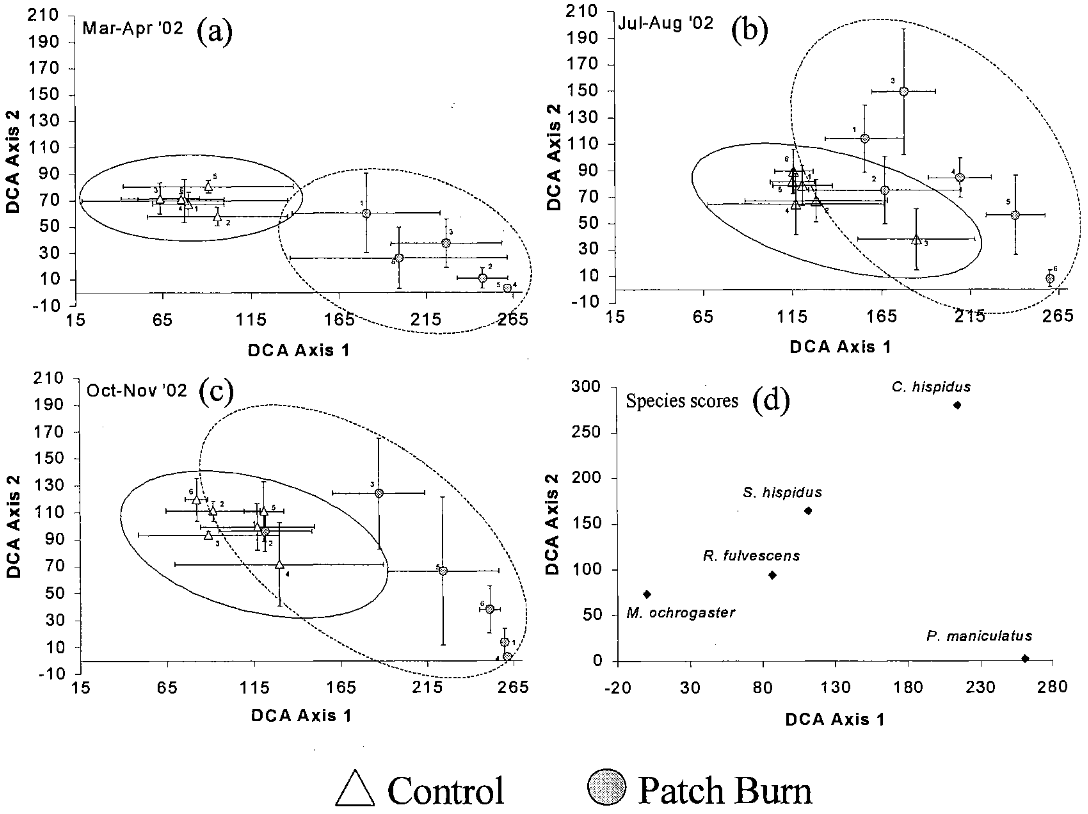
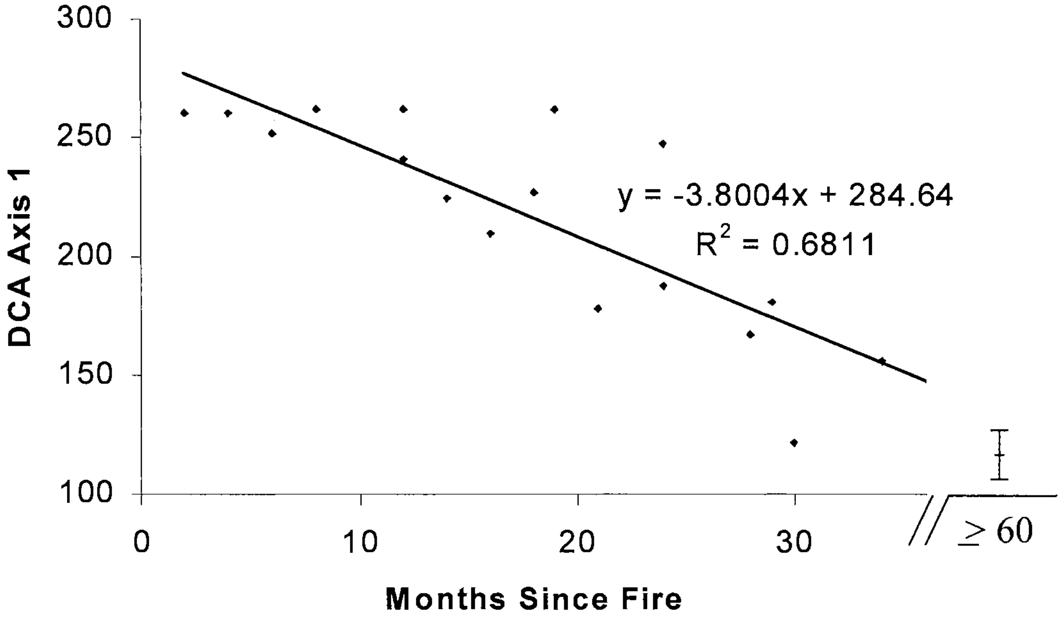

Mar-Apr '02 (a)
Jul-Aug '02 (b)
Oct-Nov '02 (c)
Species scores (d)
DCA Axis 1
DCA Axis 2
C. hispidus
S. hispidus
R. fulvescens
M. ochrogaster
P. maniculatus
△ Control
◍ Patch Burn

Figure 5. Axis-1 (top) and axis-2 (bottom) site scores, based on a detrended correspondence analysis of abundance of 5 small mammal species, as a function of number of months since burn on the Oklahoma State University Research Range, Stillwater, Oklahoma, 2002. Mean and standard error bars represent DCA axis scores for traditional treatment that are associated with time (≥ 60 months) since fire.


300
250
200
150
100
DCA Axis 1
0
10
20
30
≥ 60
Months Since Fire
y = -3.8004x + 284.64
R^2 = 0.6811

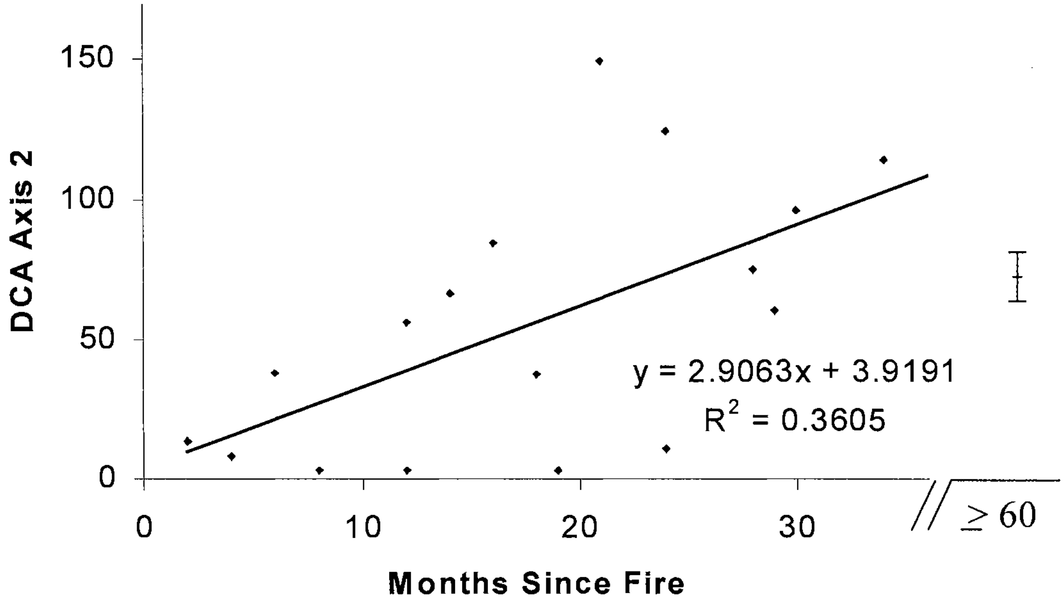

150
100
50
0
DCA Axis 2
0
10
20
30
≥ 60
Months Since Fire
y = 2.9063x + 3.9191
R^2 = 0.3605

Figure 6. Heterogeneity of control and patch burn treatments illustrated by the mean standard deviation of DCA sites scores determined the abundance of 5 small mammal species during 2002 on the Oklahoma State University Research Range, Stillwater, Oklahoma, 2002.

Traditional ☐ Patch-burn ▨

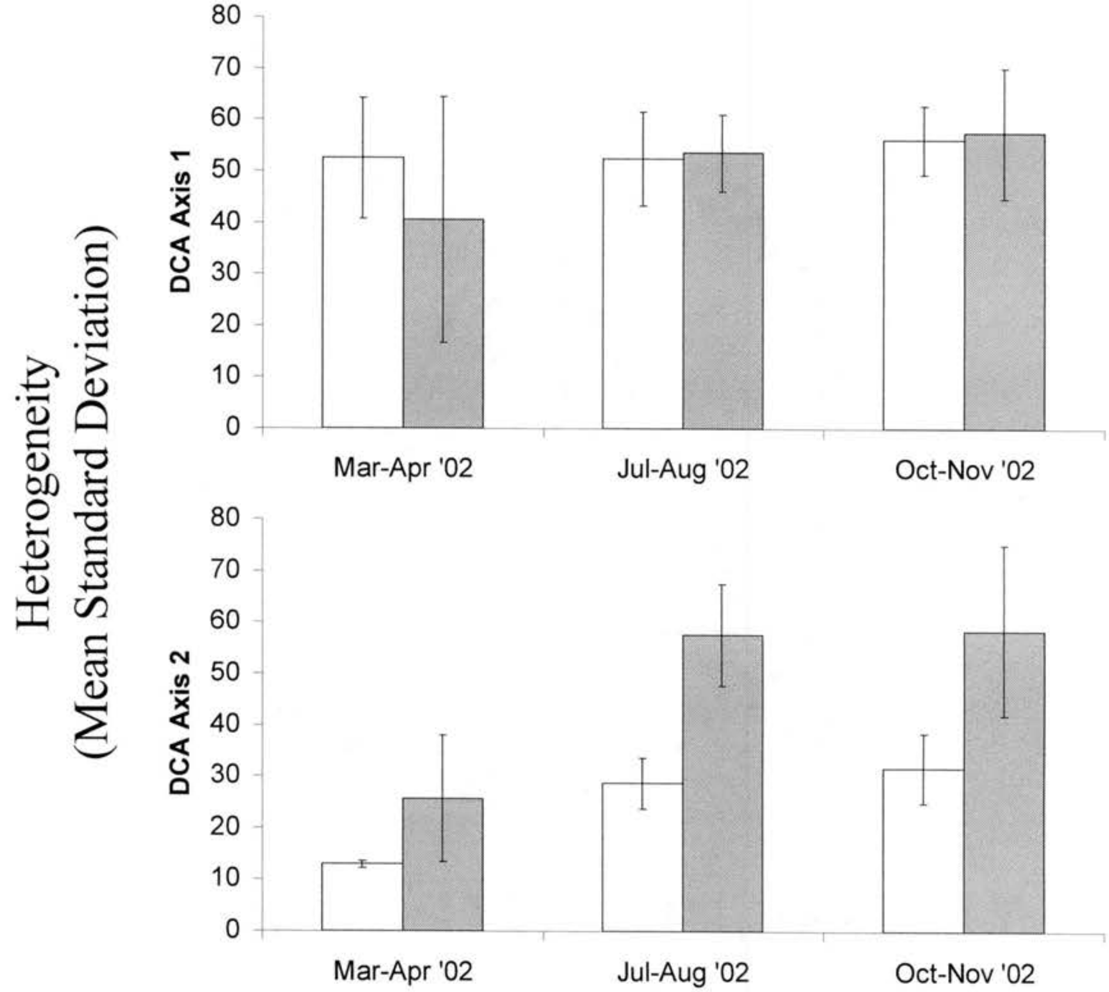
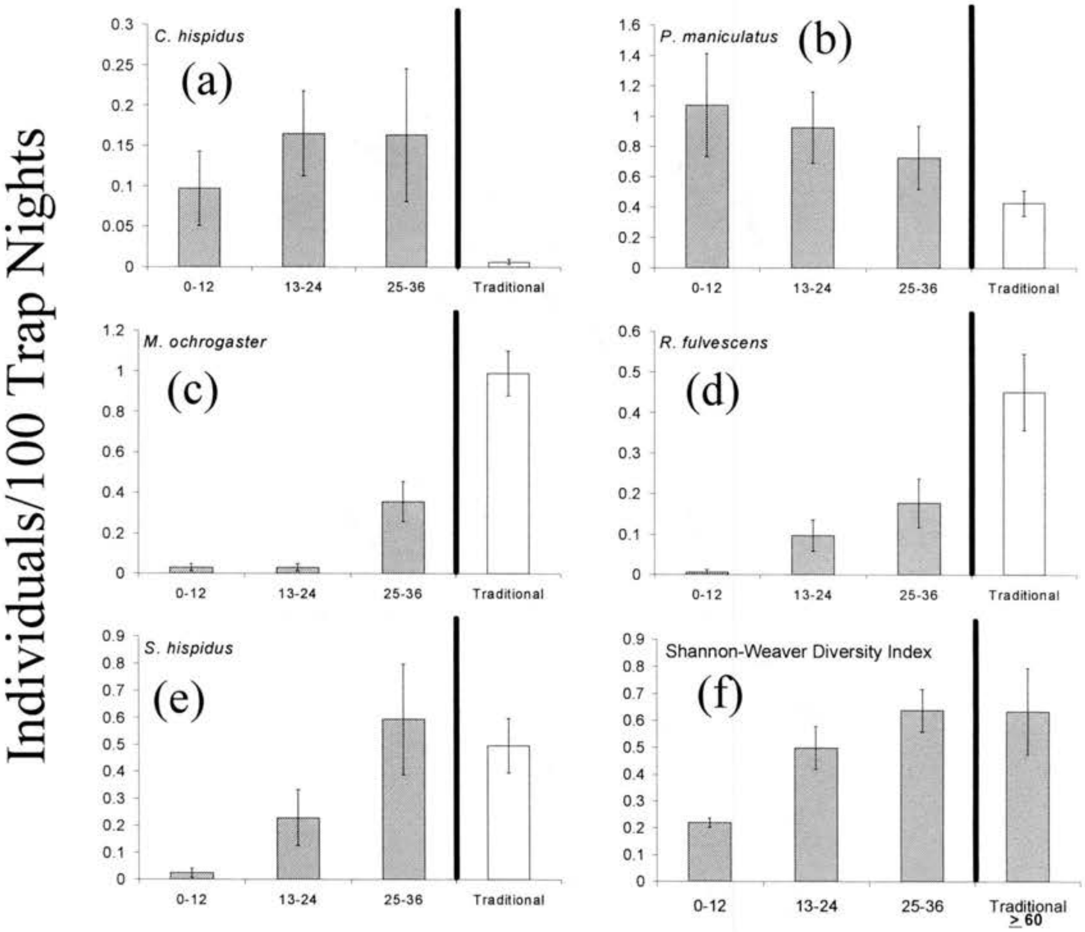

Heterogeneity
(Mean Standard Deviation)
DCA Axis 1
80
70
60
50
40
30
20
10
0
Mar-Apr '02
Jul-Aug '02
Oct-Nov '02
DCA Axis 2
80
70
60
50
40
30
20
10
0
Mar-Apr '02
Jul-Aug '02
Oct-Nov '02

Figure 7. (a-e) Relationships between capture rate and months since fire for species of small-mammals. Patch burn values are calculated from mean capture rate associated with fire history of patches that range from 0 to 60 months (n = 3). Traditional values are calculated from mean capture rate associated with a fire history ≥ 60 months (n = 3). (f) Mean species diversity index H' using the logarithmic base 10 (Shannon and Weaver 1949). Species diversity was calculated from relative abundance values that were derived from the mean number of individuals capture/100 trap nights.

Traditional ☐ Patch-burn ▨


Individuals/100 Trap Nights
(a)
C. hispidus
0.3
0.25
0.2
0.15
0.1
0.05
0
0-12
13-24
25-36
Traditional
(b)
P. maniculatus
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0-12
13-24
25-36
Traditional
(c)
M. ochrogaster
1.2
1
0.8
0.6
0.4
0.2
0
0-12
13-24
25-36
Traditional
(d)
R. fulvescens
0.6
0.5
0.4
0.3
0.2
0.1
0
0-12
13-24
25-36
Traditional
(e)
S. hispidus
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0-12
13-24
25-36
Traditional
(f)
Shannon-Weaver Diversity Index
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0-12
13-24
25-36
Traditional
≥ 60

CHAPTER 2

EVALUATING THE INFLUENCE OF GRASSLAND HETEROGENEITY ON RECOVERY AND GENERAL CONDITION OF SMALL MAMMALS

Abstract: The influence of habitat heterogeneity on physiological condition of small mammal populations was studied by simulating historical levels of heterogeneity to evaluate relationships between heterogeneity and physiological condition for several species of small mammals. We hypothesized that species of small mammals would differentially prefer habitats associated with the shifting mosaic and that those species occupying preferred habitat types would be in better physiological condition (i.e.heavier and longer bodies and lower ecto-parasite loads).

We captured 5 primary species of small mammals (1,385 individuals). Species indicator values and capture rates suggest that deer mice (*Peromyscus maniculatus*) prefer habitats associated with recently burned patches, where vegetation cover was generally reduced by fire and subsequent patch grazing, presumably because individuals associated with those habitats had greater body masses and less parasite load. Traditional patches provided an abundance of old-growth vegetation cover and a well-developed litter layer that supported more prairie voles (*Microtus ochrogaster*) and fulvous harvest mice (*Reithrodontomys fulvescens*) than did treatments associated with periodic fire and patch grazing disturbances. Condition (i.e. body mass and length) of prairie voles and fulvous harvest mice was greater in traditional treatment than on patch-burn treatment ($P \leq 0.05$). Mean relative body mass was greater in traditional treatments for prairie voles ($P = 0.001$). An inverse relationship between prairie vole and harvest mice body mass and probability of occurring within patch-burn treatment suggested that physiological condition was associated positively with high accumulation of vegetation cover and a relatively moderate or high litter layer. In general, our results indicate that habitats preferred by deer mice, harvest mice, and prairie voles were highly suitable because those habitats were associated positively with physiological condition and relative abundance. Physiological condition parameters of deer mice, fulvous harvest mice, and prairie voles suggest that these species exhibited differential competitive abilities when occupying traditional and patch-burn treatments.

Key words: *community structure; competition; distribution; habitat selection; landscape; patch; prairie; succession; variability*

INTRODUCTION

Frequency and intensity of disturbance within grassland ecosystems are critical to ecological processes, biological diversity, and heterogeneity across multiple spatial scales (Collins 1992, Fuhlendorf and Smeins 1999, Fuhlendorf and Engle 2004). Ecologists now criticize traditional land management practices that operate to minimize spatially discrete disturbances and reduce the inherent heterogeneity within managed ecosystems. Traditional grazing management practices on grasslands act to reduced the inherent levels of heterogeneity by promoting uniform distribution of grazing animals within a year (Fuhlendorf and Engle 2004), rather than restoring or increasing inherent levels of heterogeneity. The loss of such disturbances on native rangelands (associated with traditional rangeland management practices; Fuhlendorf and Engle 2001) is a contributing factor to the loss of biodiversity (Huston 1994, Christensen 1997, Ostfeld et al. 1997, Weins 1997, Fuhlendorf and Engle 2004).

Many species of small mammals depend on disturbance to create suitable habitat (Buckner and Shure 1985), and selection is strongly influenced by availability of food, shelter (Batzli 1992, Morris 1995, Hansson 1997) and probability of predation (Rosenzweig 1979, Kotler 1997). Small mammals are typically the most numerous species of mammal throughout the native prairie ecosystems of the Great Plains (Grant and Birney 1979, Rose and Birney 1985). Thus, rodent communities play a critical role in maintaining biological diversity because they not only influence vegetation communities, but they serve also as a staple food source for many mammalian and avian predators (Krebs and Myers 1974, Hornfeldt et al. 1990). Given the influence that rodent communities have on ecosystems, it is important to understand relationships between vegetation communities and small mammals to determine the efficacy of ecosystem restoration processes on sustaining or preserving ecosystems.

The evolutionary history of grasslands, in particular, suggest that grasslands are an ideal model for evaluating relationships among disturbance, heterogeneity and small mammal communities. Grassland ecosystems evolved with complex disturbance regimes that were composed of periodic large- and small-scale disturbances that were highly variable in space and time (Collins and Glenn 1997, Frank et al. 1998, Kaufman et al. 1988, Knapp et al. 1999). Because grasslands are associated with an evolutionary history of fire and grazing (Collins and Wallace 1990), we developed a heterogeneity model (Fuhlendorf and Engle 2004) that incorporates prescribed fire and ungulate grazing to restore heterogenous vegetation patterns throughout the landscape. In the absence of fire, grasslands eventually develop into shrubland and woodland vegetation (Petranka and McPherson 1979). As a result, fire is the primary ecosystem component that stabilizes native grasslands because it enhances production of C_4 grasses and deters establishment of woody plants (Gibson and Hulbert 1987, Anderson 1990, Bragg 1995).

The evolutionary history of grassland ecosystems dictates that complex interactions between local weather patterns, vegetation production, large ungulate grazing and variable fire return intervals often determine the duration and intensity of periodic fire disturbances (Cowles 1928). These disturbances maintained historical levels of heterogeneity at a variety of spatial and temporal scales (Fuhlendorf and Engle 2001, 2004). Our heterogeneity model (i.e. grazing-fire interactions) is a concept that increases heterogeneity by establishing distinct, spatially discrete vegetational patterns that continually shift throughout the landscape in space and time (Fuhlendorf and Engle 2001, 2004). According to the model, probability of fire is greatest on areas with high biomass accumulation within a grazed grassland landscape. A positive feedback occurs when a recent fire event attracts grazing animals, which further disturbs the site. A negative feedback occurs when focal grazing reduces, biomass, and therefore reduces probability and intensity of fire, which in turn lowers the probability that the patch would be subsequently grazed. Thus, grazing continually shifts through space and time as large herbivores concentrate on patches that had been burned more recently, allowing the successional progression of previous patches (Fuhlendorf and Engle 2001, 2004). These disturbance patterns also can have profound influences on wildlife population dynamics

(Wiens 1976), animal movement patterns (Forman and Godron 1986, Gustafson and Gardner 1996), further complicating plant and animal interactions associated with heterogeneity. In fact, heterogeneity may act to stabilize ecological systems by influencing predator-prey or parasite-host interactions, minimizing the spread of disturbances, pests, or pathogens, and thereby stabilizing population dynamics and enhancing species diversity (Taylor 1991, Huston 1994, Rosenzweig 1995). Landscape variability associated with plant, animal and fire interactions can lead to a shifting mosaic in which, the presence of variable habitat types attracts different species and likely provides complementary resources (i.e. food availability, protection from wind, snow and ice) for individual species that have multiple habitat requirements, presumably enhancing habitat quality and biodiversity. These alternative resources may have been critical to species survival during times of severe climatic stress.

Extreme winter temperature has been attributed to density reductions and local extinctions of small-mammal populations throughout the central Great Plains (Sauer 1985, Langley and Shure 1988). Prior to the onset of our study, average statewide temperatures during December 2000 (-0.7 °C) represented Oklahoma's coldest month in nearly 17 years (National Climatic Data Center 2000, Clark et al. 2003). Those extreme winter temperatures provided a unique opportunity to determine the influence of heterogeneity on relative abundance and subsequent recovery of small-mammals following a severe climatic event. Statewide evidence suggests that extreme winter temperatures likely had a negative influence on small-mammal populations throughout my study site. Accumulations of snow and ice persisted for about 5 days in mid-December across much of central and eastern Oklahoma, followed by > 12 cm of additional snow on 31 December 2000 (National Climatic Data Center 2000), likely restricting foraging opportunities for many species of small mammals and presumably depleting energy reserves leaving many individuals susceptible to starvation and eventual mortality.

I used this as an opportunity to evaluate the recovery (i.e. population response) of several species of small mammals to patch-burn management designed to increase or maintain historical levels of heterogeneity. Specifically, our objective was to evaluate relationships of small-mammal communities with habitat selection, physiological condition and recovery of small-mammal communities associated with grassland ecosystems following a local population decline. We hypothesized that species of small mammals would differentially prefer habitats associated with the shifting mosaic and that those species occupying preferred habitat types would be in better physiological condition (i.e. these individuals would likely be associated with higher body weight, longer body lengths and/or lower parasite loads).

MATERIALS AND METHODS

Study area.−Research was conducted on the Oklahoma State University Range Research Station that is located approximately 21 km southwest of Stillwater, Oklahoma and consists of 1400 ha of native grassland and cross timbers. Most of this area is classified as typical of tallgrass prairie in a high seral stage, but some local communities are representative of Cross Timbers vegetation (*Quercus stellata, Q. marilandica*, and

Juniperus virginiana). Dominant grasses included little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*) and indiangrass (*Sorghastrum nutans*). Secondary grasses included switchgrass (*Panicum virgatum*), tall dropseed (*Sporobolus asper*), sideoats grama (*Bouteloua curtipendula*) and Scribner's dicanthelium (*Dicanthelium oligosanthes*). The dominant forbs were western ragweed (*Ambrosia psilostachya*) and common broomweed (*Gutierrezia dracunculoides*). Taxonomic nomenclature follows Hatch et al. 1990.

To determine associations between heterogeneity and the distribution of small-mammal communities within tallgrass prairies of the central Great Plains, we used a completely randomized design that included 3 replicated pairs of pastures (Patch Burn and Traditional Treatments) on the Oklahoma State University Range Research Station. Pastures ranged in size from 50–60 ha and were divided into 6 equal patches (ca. 8.3–10 ha.) that were delineated at the corners by permanent markers (metal t-posts) designed to facilitate ecological monitoring, but not to interfere with livestock or wildlife behavior and distribution. The patch treatment was established by 1) rotating spring and fall burns that consumed 1/6 th of the pasture seasonally (i.e. 1/3 rd annually, resulting in a 3-year fire return interval). The corresponding traditional treatments were not burned and were assigned to treatment pastures according to their similarity in total woody cover. Experimental units (i.e. pastures) of both traditional and patch burn treatments were moderately grazed by free-ranging stocker cattle ($\bar{x}$ = 270 kg) at 3.0 ha/animal from 1

December to 31 September and were treated similarly except for the application of spatially discrete fires in the patch treatment.

Small-mammal sampling. – Species of small mammals were censussed about every 2.5 months on each patch of each treatment during May–Jun, Aug–Sep, Nov–Dec of 2001 and Mar–Apr, Jul–Aug, and Oct–Nov of 2002. One sampling period covered a span of 18 days. Thus, to prevent any bias associated with changes in weather patterns (i.e. temperature or rainfall that are likely to influence trap success) throughout an 18-day sampling period, patch burn and traditional patches were censussed simultaneously. For instance, replicated patch pairs were established (i.e. treatment patch # 1–6 corresponded to a traditional patch # 1–6), where experimental units with identical patch numbers constituted 1 patch pair per replication (i.e. patch pair # 1 = treatment patch #1 + traditional patch # 1 for each of 3 replications; Fig. 1b). Trapping occasions were subdivided so that one patch pair was sampled concurrently. Replicated patch pairs were selected randomly (RANUNI, SAS Institute, Inc. 2000) and censussed using 2, 40 x 40 m grids per patch that were placed randomly in tallgrass prairie habitat (5 x 5 trapping grid with 10-m spacing). Each grid contained 25 traps and one trapping occasion was restricted to one patch pair per replication (i.e. 100 traps/patch pair per replication or 300 traps). Each sampling period required 6 trapping occasions (i.e. 6 patch pairs/replication) where each trapping occasion was sampled for 3 consecutive nights (i.e. 1 sampling period requires 18 trap nights; Fig. 1b).

Mammals were trapped with Sherman live-traps (7.6 x 8.9 x 22.9 cm) baited with rolled oats and supplied with cotton for bedding during fall and winter trap sessions. Upon capture each animal was identified to species, sex and age (adult or juvenile) were determined and each individual was marked by toe-clipping and with a numbered aluminum ear tag (National Band and Tag Co., Lexington, KY). Rodent trapping conformed to guidelines sanctioned by the American Society of Mammalogists (Animal Care and Use Committee 1998). Gender, body mass, total length of body and tail, length of hind foot, ear length, and relative mass (body mass/body length^3) was computed to determine general condition of rodent species. Reproductive status (pregnant, lactating, or neither for females; scrotal or non-scrotal for males) and general condition parameters (# of ecto-parasites or external wounds) also were recorded. Females that were pregnant or lactating and scrotal males were classified as reproductively active. Females were considered lactating if mammary tissues were conspicuous with hair-free areas surrounding the nipples (McMurry et al. 1994). We estimated relative density as the number of animals caught per 100 trap-nights. A trap-night was defined as one functional trap open for one 24-h period (McMurry et al. 1994). To account for variation in sprung traps among sites, traps found sprung and empty were subtracted from analyses (McMurry et al. 1994).

Statistical analysis.–Our analyses were based on captures/unit effort to account for sprung traps and variation in effort among sites. We used analysis of variance (PROC ANOVA, SAS Institute, Inc. 2000) to test the null hypotheses that there are no differences in pooled capture rates (captures/100 trap nights) among treatments and that there are no differences in general condition parameters of each species among treatments. We used logistic regression model using stepwise forward selection of variables to determine if body condition parameters were significant predictors of probability of occurrence (Hosmer and Lemeshow 1989) within patch burn pastures (P_{OPB}). Variables were permitted to enter and remain in the model in a hierarchical fashion when the $\log_e$ likelihood was deemed appropriate ($\alpha = 0.15$; Hosmer and Lemeshow 1989, Mickey and Greenland 1989, Bowyer et al. 1999). We tested the suitability of our logistic regression model using a Hosmer-Lemeshow test for goodness-of-fit (Hosmer and Lemeshow 1989:140) where $P > 0.05$ indicated the model fit. A significance level of $\alpha < 0.05$ was set for all appropriate tests.

RESULTS

Recovery

Capture rates throughout 2001 were extremely low ($\bar{x} = 2.2$ captures/100 TN) and progressively increased throughout 2001 (Fig. 2). Capture rates continued to increase in 2002 and reached its peak in August 2002 at 6.9 captures/100 trap nights. Capture rate was greater on traditional treatments in 4 of 6 trap sessions and our results suggest that small mammal populations associated with traditional treatments recovered at a faster rate than those populations associated with patch burn treatments.

Community Composition

Landscape-Level Responses– We captured 7 species (1,399 individuals) of small mammals. Two species (*Peromyscus leucopus*, n = 6; *Reithrodontomys montanus*, n =

8), representing 1% of captures, were collected incidentally and were excluded from analyses. As a result, our analyses were based on 1,385 individuals. There were significant differences in capture rate among the five species of small mammals throughout our study period. Mean captures/100 trap nights for deer mice ($\bar{x}$ = 0.46) and prairie voles ($\bar{x}$ = 0.43) were higher than for other species and suggests that these species dominated the small-mammal community. Capture rates for cotton rats ($\bar{x}$ = 0.26) and fulvous harvest mice ($\bar{x}$ = 0.22) were higher than hispid pocket mice ($\bar{x}$ = 0.05, $P \leq 0.05$).

Capture rates for hispid pocket mice were greater in patch burn than in traditional treatments in 5 of 6 trap sessions. Similarly capture rates for deer mice were greater within patch burn treatments than in traditional treatments that were not burned in 4 of 6 trap sessions (Fig 2). However, capture rates were greatest on traditional treatments for fulvous harvest mice, and cotton rats during 4 of 6 trap sessions suggested that these species are primarily associated with traditional patch treatments (Fig. 2). Capture rates associated with prairie voles were greater on traditional than patch burn treatments during the entire study period (Fig. 2).

The number of pooled captures/unit effort was greatest in small-mammal communities from unburned areas than from areas that were patch burned in 3 of 6 trapping sessions (Fig. 2). Pooled capture rates associated with traditional treatments did not differ between trapping sessions from November 2001 through November 2002 (Fig. 2). Capture rates associated with patch-burn treatments did not differ between trapping sessions from May–September 2001, November 2001–April 2002 and from April 2002 –November 2002 (Fig. 2), suggesting that capture rates stabilized during 2002.

Physiological Condition

Physiological condition parameters follow predictable patterns associated with our abundance data. For instance, mean body mass was greater and parasite load was lower on patch-burn treatments for deer mice which was also the treatment where this species was most abundant (Table 1). Relative body mass also was greater within patch burn compared with traditional treatments, but the difference was not significant ($P = 0.077$; Table 1). However, general condition parameters (body mass and length) for species of prairie voles and fulvous harvest mice were greater on traditional treatments than on patch burn treatments which is where they are most abundant ($P \leq 0.05$; Table 1). Mean relative body mass was greater in traditional treatments for prairie voles ($P = 0.001$). Although differences (between experimental units) associated with relative body mass (body mass/ body length) did not meet our significance level ($P \leq 0.05$), mean relative body mass tended to be greater in patch burn patches for deer mice and tended to be greater in traditional patches for fulvous harvest mice ($P < 0.10$). All other general condition parameters did not differ between treatments for species (Table 1).

Stepwise logistic regression analysis ($\chi^2 = 11.54$, $d.f. = 1$, $P = 0.001$) selected ecto-parasite load and body mass as the best predictors of patch burn occurrence (Table 2) where individuals of deer mice that have the lowest ecto-parasite load and highest body weight were most likely to occur in patch burn treatments (Table 3), suggesting that fire may contribute to greater condition indices for this species. The Hosmer-Lemeshow test for goodness-of-fit indicated that the model fit the data well ($\chi^2 = 4.43$, *d.f.* = 7, P = 0.730). Univariate logistic regression indicated a positive relationship between probability of occurrence in patch burn treatments (P_{OPB}) and body mass ($\chi^2 = 5.21$, *d.f.* = 1, P = 0.023), and an inverse relationship between P_{OPB} and ecto-parasite load ($\chi^2 = 11.33$, *d.f.* = 1, $P = 0.001$) for deer mice (Fig. 3). Ecto-parasite loads were correlated negatively with tail length ($r = 0.10$, $P = 0.030$) in prairie voles. Further, univariate logistic regression indicated also an inverse relationship between (P_{OPB}) and body mass in prairie voles (χ^2 = 11.24, d.f. = 1, $P = 0.001$), and fulvous harvest mice ($\chi^2 = 5.43$, d.f. = 1, $P = 0.020$; Fig. 3).

DISCUSSION

Evidence Supporting a Decline and Subsequent Recovery

Local extreme winter conditions can directly influence small-mammal communities and therefore may indirectly modify long-term ecological processes such as population cycles associated with predator-prey relationships or herbivory relationships between plant and animals that can negatively influence woody plant recruitment within grassland ecosystems (Davidson 1993, Ostfeld and Canham 1993, Ostfeld et al. 1994, 1997). Extreme winter conditions that persisted throughout December and January of 2000 and 2001 likely caused dramatic statewide population declines of small mammals. This unique climatic event provided an excellent opportunity to evaluate the influence of heterogenous grassland ecosystems on the recovery of small mammal communities. Although these extreme environmental events occurred prior to the onset of our study, statewide evidence suggested that many small-mammal communities experienced population declines and communities residing on our study site were no exception. Capture rates of small mammals were reduced throughout central and eastern Oklahoma in the days and months following the winter storms of 2000. For instance, capture successes in Payne County, Oklahoma, were documented as high as 20–30 captures/100 trap nights prior to the winter storms of 2000–2001 but were subsequently reduced to 1 captures/100 trap nights during October 2001 (Clark et al. 2003). Similarly, capture success at the Tallgrass Prairie Preserve declined from 2.2 captures/100 trap nights in early December 2000 to 0.0 captures/100 trap nights during monthly sampling periods from January to November 2001 (Clark et al. 2003).

Our evidence (collected immediately following the winter storms of 2000) lends further support for the massive statewide population declines. For instance, capture rates throughout 2001 average only 2 captures/100 trap nights and progressively increased throughout 2001 (Fig. 2). Capture rates continued to increase in 2002 and reached its peak in August 2002 at 7 captures/100 trap nights. Capture rate was greater on traditional treatments in 4 of 6 trap sessions and our results suggested that small mammal populations associated with traditional treatments recovered at a faster rate than those populations associated with patch-burn treatments. For instance, capture rates did not differ during our first trap session in May-Jun ‘01, but were greater in traditional than in patch burn treatments throughout the following 4 trap sessions. Evidence suggests that patch burn communities began to recover by Mar-Apr '02, while traditional treatments showed signs of recovery 3 – 4 months prior to those communities associated with patch burn treatments (Nov-Dec '01; Fig. 2).

Population Distribution and Physiological Condition

Superior habitats are generally described as those habitat types that provide a high abundance of resources (i.e. food abundance, protection from predators) and maximize individual fitness (Van Horne 1983, Ostfeld 1985, Ostfeld and Kosterman 1986). Our model attempts to restore historical patterns of heterogeneity that were associated with native prairie habitats that have an evolutionary history of grazing and fire (Fuhlendorf and Engle 2001, Knapp et al. 1999, Diamond et al. 1995, Axelrod 1985). Historical habitat types presumably maximized biodiversity because they likely supplied a vast assortment of patch types that were inhabited by numerous species each with specific habitat preferences. Different habitat types within spatially heterogenous landscapes vary in their quality depending on species preferences. Therefore, it is reasonable to assume that when species are not of equal competitive ability, dominant individuals will demonstrate a preference for high-quality habitats and inferior individuals will be forced to occupy low-quality habitats that provide inferior resources and protection from predators, ultimately decreasing fecundity (Fretwell and Lucas 1970). Thus, analysis of body condition parameters (i.e. body mass, body length, etc.) can be useful indicators to differentiate between high and low-quality habitats because they can be highly correlated with an individuals nutritional status and can directly influence survival and reproductive success (Atkinson and Ramsay

1995). Body condition refers to an animal's energetic state, in which an animal in superior condition has higher energy reserves than an animal in poor body condition (Millar and Hickling 1990). Thus, assessment of physiological condition of wild animals in the field can be a critical component to evaluate habitat quality for specific species.

Rodents should exploit only those resource patches that have an ideal balance between adequate foraging opportunities and risk of predation (Brown 1992, Schmidt and Brown 1996, Schmidt et al. 2001). Several hypothesis have been proposed to describe the mode of habitat selection based on the resulting fitness patterns among small mammals. The ideal free distribution hypothesis was derived to describe the mechanisms of habitat selection when habitats differ in quality. Animals that have free and equal access to all available habitat patches choose sites that maximize fitness and stabilize population distributions, so that they exhibit little variation in fitness among individuals (Fretwell and Lucas 1970, Fretwell 1972). Populations that experience declines in fitness with increased density, should settle among available habitat types such that their fitness is equalized. Populations associated with these characteristics are characterized as exhibiting an ideal free distribution (Fretwell and Lucas 1970, Milinski and Parker 1991, Abramsky et al. 2000). Alternatively, the ideal despotic distribution and the truncated phenotypic distribution hypotheses predict that the best competitors will occupy higher quality habitats. Thus, high quality habitats (i.e. where resource availability and gains in fitness are maximized) are likely defended by dominant individuals and subordinates are forced to occupy lower quality habitat types where the balance between resource availability and predation risks are less advantageous (Fretwell and Lucas1970, Sutherland and Parker 1985, 1992, Parker and Sutherland 1986, Milinski and Parker 1991). As a result, phenotypes become split between habitat types where those occupying the higher quality habitats are likely to be in better physiological condition (i.e. higher body weights), thereby gaining a competitive advantage over less physical individuals and likely force subordinate individuals to occupy lower quality habitats. Thus, individuals with access to high-quality habitats tend to gain fitness advantages over individuals occupying areas with limited resource availability.

We were able to document the influence of landscape heterogeneity and distinguish between high- and low-quality habitats for 3 species of small mammals (deer mice, prairie voles, fulvous harvest mice). Our data suggested that spatial patterns of abundance and short-term dynamics for small-mammal communities within our study site were highly influenced by periodic disturbances. Small-mammal responses associated with experimental units followed expected patterns in response to periodic fires as previously reported (Kaufman et al. 1990, Clark and Kaufman 1990). Species indicator values and capture rates suggests that deer mice prefer habitats associated with recently burned patches within the patch burn treatments. Capture rates of deer mice and hispid pocket mice were greatest on patch burn treatments than on traditional treatments in 4 of 6 trap sessions (Fig. 2). Deer mice generally prefered habitats associated with open prairies that were free of woodlands and increases in abundance on recently burned sites is highly documented (Kaufman et al. 1983, Schramm and Willcutts 1983, Snyder and Best 1988).

Similarly, hispid pocket mice also prefer habitats associated with exposed soil and limited vertical structure (Kaufman et al. 1988, Paulson 1988, Clark et al. 1998). Our findings suggest that deer mice and hispid pocket mice have positive responses to temporal changes in landscape heterogeneity at the local patch level (driven by time since fire), supporting observations of Langley and Shure (1988). These results were in accordance with predilections of deer mice for grassland habitats (Kaufman et al. 1983, Schramm and Willcutts 1983, Snyder and Best 1988, Kaufman et al. 1990). Similarly, traditional patches provided an abundance of old growth vegetation cover and a well developed litter layer that supported higher abundances of prairie voles and harvest mice than did treatments associated with periodic fire and grazing disturbances, supporting previous reports of habitat preferences for these species (Kaufman and Fleharty 1974, Spencer and Cameron 1982, Clark et al. 1998).

Because relative abundance or population densities alone are insufficient to classify habitat suitability (Van Horne 1983), we defined suitability in terms of physiological condition and potential reproductive output. Reproductive success of mammals is highly correlated with body condition, where individuals in superior condition generally benefit by increasing litter mass, number of litters, neonatal mass, and an increase in breeding life-span (Atkinson and Ramsay 1995, Wauters and Dhondt 1995). Individuals of deer mice that were associated with higher body mass and lower parasite loads were most likely to occur in patch burn treatments where vegetation cover was generally reduced by fire and subsequent patch grazing. However, abundant vegetation cover (associated with traditional patches) may have reduced predation risk and increased foraging opportunities for prairie voles and harvest mice (Brown 1992, Morris 1984). The inverse relationship between body mass and probability of occurring within patch burn treatments for prairie voles and harvest mice suggested that physiological condition was associated positively with high accumulation of vegetation cover and a relatively moderate to high litter layer. Harvest mice and prairie voles generally prefer patches with moderate or high litter cover for foraging and nesting and in fact, deer mice tend to be less efficient foragers than harvest mice in patches with a dense litter layer, presumably because smaller body size allows harvest mice to forage more efficiently within dense vegetation layers (Kaufman and Kaufman 1990).

To maintain adequate energy reserves females require a 2-fold increase in food consumption to support the rigorous energetic demands required for successful reproduction (Glazier 1985, Lochmiller et al. 1982). In general, our results indicate that habitats preferred by deer mice, harvest mice, and prairie voles were highly suitable because those habitats were associated positively with physiological condition and relative abundance. We documented that body mass, relative body mass, and body length was greatest within preferred habitats for 3 of 5 rodent species, presumably because individuals with superior competitive abilities realized that those habitats supplied an abundance of food resources and adequate relief from predation and parasitism (Fretwell 1972). As a result, high-quality habitats were likely defended by superior individuals, where subordinates were forced to occupy inferior habitat types.

Habitat characteristics (i.e. availability and distribution of food, potential mates, and protective cover) are the primary factors that modify habitat selection of rodent species (Ostfeld 1985). The ideal free distribution hypothesis is a theory of habitat selection that is applied when habitat selection acts to stabilize the distribution and general condition parameters (fitness) of individuals across all habitat types (Fretwell and Lucas 1970). Alternative hypotheses to the ideal free distribution have been proposed to explain instances when habitat selection results in situations where subordinate individuals are forced to occupy lower quality habitats. Two such hypothesis include the ideal despotic distribution that predicts the best competitors will occupy the highest-quality habitats and will ultimately gain fitness advantages over less competitive individuals occupying low-quality habitats (Fretwell and Lucas 1970) and the truncated phenotypic distribution is a modification of the despotic distribution that predicts a distinctive phenotypic advantage (i.e. body weight, body length, parasite load) occurs when the best competitors occupy the highest-quality habitats (Milinski and Parker 1991).

Analysis of our data suggests that habitat preferences of 3 species of small mammals support the ideal despotic distribution (Fretwell and Lucas 1970) and the truncated phenotypic distribution (Milinski and Parker 1991) hypotheses. For instance, previous population studies of deer mice suggest that adults are highly territorial (Wolff et al. 1983, Wolff 1985). When dominant individuals occupy and defend a proportion of resources located within high quality habitats they force subordinate individuals to occupy inferior habitats that ultimately influences individual fitness (Davies and Houston 1984, Pusenius and Schmidt 2002). Further, after all resources associated with high quality habitats have been utilized, then individuals are expected to occupy habitats in order of decreasing quality and subordinates should correlate positively with total density (Messier et al. 1990, Tregenza et al. 1996). Therefore, positive associations between capture rate and habitat type (traditional patch or patch burn) suggested that subordinate individuals may be constrained by territoriality of dominant individuals, lending support for ideal despotic distribution hypothesis (Fretwell 1972). Otherwise, to support the ideal free distribution, capture rates should settle across all treatments such that physiological differences between habitats are negligible, ultimately equalizing fitness among all available habitats.

However, our data suggests that fitness as predicted by general condition parameters did not settle across all habitat types or treatments. Rather, individuals inhabiting their preferred habitat types (as suggested by previous reports) were generally in better physiological condition than those occupying lower quality habitats. Differences associated with general condition parameters (i.e. body mass, parasite loads) can indicate differential competitive abilities across habitat patches (Milinski and Parker 1991). On our study site, physiological condition parameters of deer mice, harvest mice, and prairie voles suggested that these species exhibited differential competitive abilities between traditional and patch burn patches. As a result, the distribution of phenotypic parameters that diverged between individuals occupying traditional vs. patch burn habitat types suggested that individuals occupying their preferred habitats (i.e. patch burn patches for deer mice vs. traditional patches for harvest mice and prairie voles) are likely to increase their reproductive output, presumably because they tend to be in better physiological condition, lends support for the truncated phenotypic hypothesis. Similar results have been reported for species of meadow voles (*Microtus pennsylvanicus*) where habitat selection between mowed and unmowed patches suggested that individuals in superior physiological condition forced subordinates to occupy low-quality, mowed habitats (Pusenius and Schmidt 2002). Our data supports two primary hypotheses (ideal despotic distribution, truncated phenotypic distribution) on habitat selection for species of deer mice, harvest mice, and prairie voles, and argues against the ideal free distribution hypothesis for these species. However, relative abundances and physiological condition parameters of cotton rats were relatively consistent between traditional and patch burn patches, implying equal fitness across all habitats and lending support for the ideal free distribution hypothesis.

Conclusions

I discussed associations between traditional and patch-burn patches and habitat selection for 5 primary species of rodents. It is clear that management techniques designed to restore historical levels of heterogeneity can influence distribution and abundance of small mammal populations. We have argued that individuals of deer mice, harvest mice, and prairie voles tend to prefer habitat types that are consistent with previously reported habitat preferences. We further argue that those individuals with a competitive advantage likely occupied high-quality habitats and forced subordinate individuals into inferior habitats that ultimately may have influenced their reproductive output. This pattern of habitat selection argues against the ideal free distribution and lends support for the ideal despotic distribution and/or the truncated phenotypic distribution described by Fretwell (1972) and Milinski and Parker (1991), respectively. Caution should be used when interpreting the significance of traditional vs patch burn management techniques on species of small mammals without considering the spatial scale at which these processes are observed. Because analysis of multiple scales are necessary to accurately describe relationships between organisms and their environment (Fuhlendorf and Smeins 1996, 1999), it is important to note that this study was conducted at a landscape scale, where habitat patches created by patch burning were considerably greater than the home ranges for these species of small mammals. Therefore, further study is warranted to determine whether this pattern would be found at smaller spatial scales (i.e. where a mosaic of habitat types occurred within a species home range) and to better understand the influence of habitat heterogeneity on the distribution and abundance of small mammal assemblages.

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Table 1. General condition parameters associated with traditional patch and patch burn treatments for species of small mammals on the Oklahoma State University Range Research Station, Stillwater, Oklahoma, 2001–2002.

Species	Unburned Control			Patch Burn			
Variable	*n*	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*P*
C. hispidus							
Body mass (g)	1	35		39	38.3	1.45	0.723
Body length (mm)	1	103.2		39	89.9	1.41	0.145
Tail length (mm)	1	87.7		39	87.8	1.36	0.993
Ear length (mm)	1	9.5		38	10.1	0.27	0.713
Hind foot length (mm)	1	23.6		41	22.2	0.28	0.437
Body mass/body length (g/cm^3)	1	0.03		39	0.05	<0.00	0.115
Ecto-parasite load (#)	1	0		41	0.27	0.12	0.734
P. maniculatus							
Body mass (g)	165	15.4	0.33	257	16.7	0.46	0.033
Body length (mm)	165	73.7	0.61	258	74.1	0.51	0.605
Tail length (mm)	165	50.3	0.63	258	51.4	0.59	0.218
Ear length (mm)	164	11.7	0.08	256	11.6	0.06	0.206
Hind foot length (mm)	166	17.2	0.10	255	17.2	0.08	0.972
Body mass/body length (g/cm^3)	165	0.05	0.01	257	0.06	0.01	0.077
Ecto-parasite load (#)	166	1.1	0.24	256	0.1	0.05	<0.001
M. ochrogaster							
Body mass (g)	413	35.6	0.51	38	30.2	1.39	0.002

Table 1. Continued

Species	Unburned Control			Patch Burn			
Variable	*n*	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*P*
Body length (mm)	414	101.8	0.59	38	94.2	3.16	0.001
Tail length (mm)	414	29.6	0.32	38	27.3	0.61	0.040
Ear length (mm)	391	10.8	0.06	36	10.1	0.15	0.003
Hind foot length (mm)	414	17.4	0.06	38	17.3	0.17	0.752
Body mass/body length (g/cm^3)	413	0.03	<0.00	38	0.73	0.69	0.001
Ecto-parasite load (#)	414	0.46	0.06	38	0.42	0.18	0.847
R. fulvescens							
Body mass (g)	173	13.4	0.22	23	11.9	0.66	0.019
Body length (mm)	173	65.3	0.54	23	62.2	1.77	0.053
Tail length (mm)	173	81.2	0.64	23	75.6	2.63	0.006
Ear length (mm)	171	10.9	0.08	23	10.3	0.46	0.031
Hind foot length (mm)	171	18.1	0.07	23	17.8	0.34	0.125
Body mass/body length (g/cm^3)	173	0.05	<0.00	23	0.19	<0.00	0.057
Ecto-parasite load (#)	174	0.33	0.16	23	0.09	0.09	0.596
S. hispidus							
Body mass (g)	128	105.4	4.23	51	95.7	7.10	0.229
Body length (mm)	129	129.3	1.62	51	123.8	3.03	0.090
Tail length (mm)	129	87.3	1.42	51	89.4	2.02	0.418
Ear length (mm)	127	15.2	0.14	47	15.2	0.22	0.964
Hind foot length (mm)	129	26.6	0.34	50	26.4	0.54	0.736

Table 1. Continued

Species	Unburned Control			Patch Burn			
Variable	*n*	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*P*
Body mass/body length (g/cm^3)	128	0.05	<0.00	51	0.05	<0.00	0.379
Ecto-parasite load (#)	129	5.2	3.67	50	0.84	0.35	0.460

Table 2. Logistic-regression model and analysis of maximum-likelihood estimates for occurrence of *P. maniculatus* in patch burn treatments on the Oklahoma State University Range Research Station, Stillwater, Oklahoma, 2001–2002.

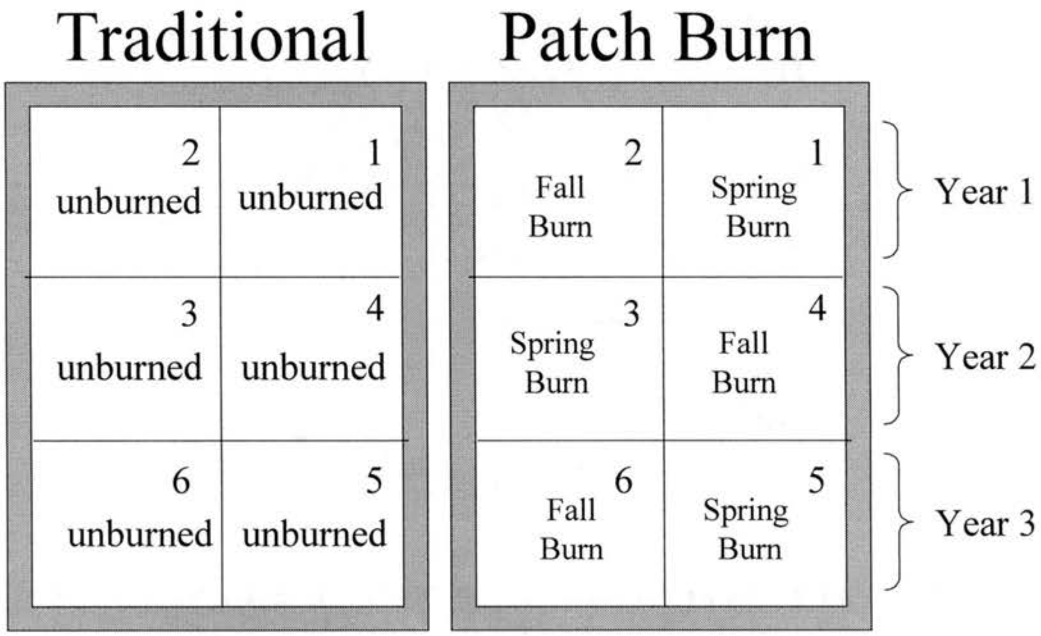
Parameter	Estimate	*SE*	χ^2	*P*
Intercept	-0.5657	0.48	1.39	0.239
Ecto-parasite (#)	-0.3560	0.10	11.54	<0.001
Body mass (g)	0.0725	0.03	5.80	0.016

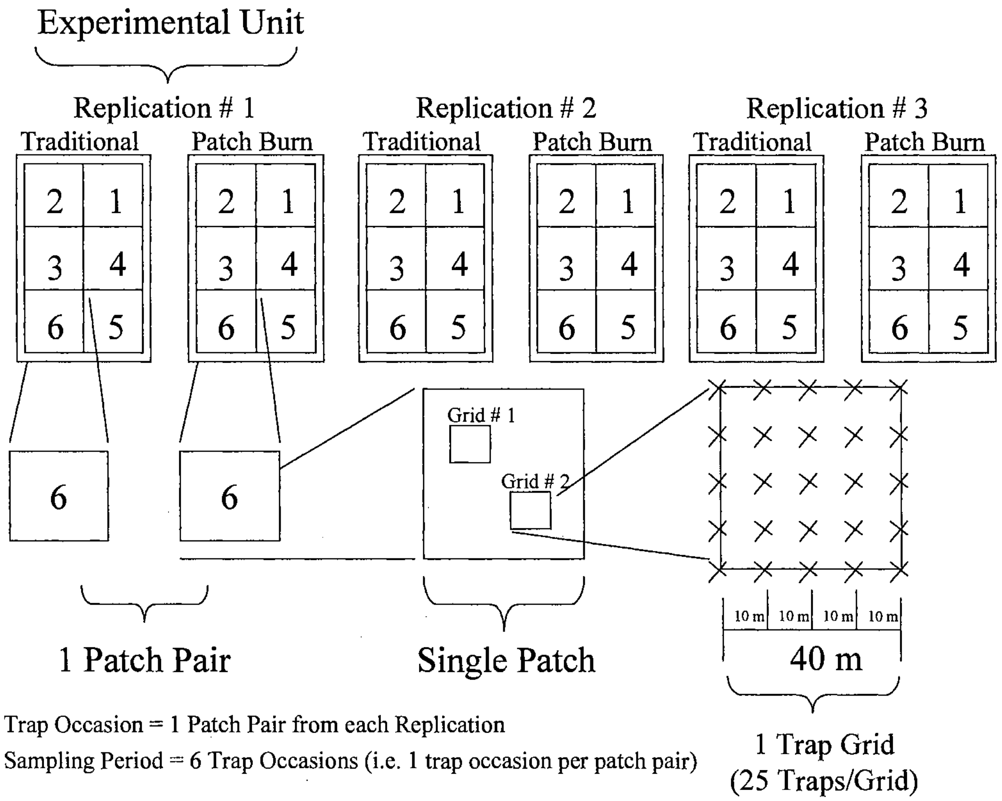
Table 3. Predicted probability of *P. maniculatus* occurring in patch burn treatments on the Oklahoma State University Range Research Station, Stillwater, Oklahoma, 2001–2002, as a function of parasite load and body mass, using a logistic model[a].

Ecto-parasite load	Body mass (g)					
(#)	10	20	30	40	50	60
0	0.54	0.71	0.83	0.91	0.96	0.98
1	0.45	0.63	0.78	0.88	0.94	0.97
5	0.17	0.29	0.46	0.64	0.78	0.88
10	0.03	0.06	0.12	0.23	0.38	0.56
20	<0.00	<0.00	<0.00	0.01	0.02	0.03

[a] P (occurring in patch burn treatments) = $e^a / 1 + e^a$, where a = [-0.5657 + 0.0725 (body mass) − 0.3560 (parasite load)].

Figure 1. Schematic of the experimental design of 3 replicated treatments (traditional, patch burn) and a graphic illustration identifying locations of trapping grids on the Oklahoma State University Research Station, Stillwater, Oklahoma. The bold outer rectangles represent pasture boundaries (≈ 60 ha), while the inner rectangles represent the boundaries of 6 equal patches (≈ 10 ha). (a) Patches associated with patch burn treatments were established by 1) prescribing spring and fall fires to 1/3 rd of the pasture annually, resulting in a 3-year fire return interval. Patches within traditional treatments were associated with a fire return interval ≥ 60 months and remained unburned throughout our study. (b) Replicated patch pairs were established, where experimental units with identical patch numbers constituted 1 patch pair per replication. Trapping occasions were subdivided so that one patch pair was sampled concurrently and censussed using 2 40 x 40 m grids per patch that were randomly placed in tallgrass prairie habitat (5 x 5 trapping grid with 10-m spacing). Each grid contained 25 traps and one trapping occasion was restricted to one patch pair per replication (i.e. 100 traps/patch pair per replication or 300 traps across all replications). Each sampling period required 6 trapping occasions (i.e. 6 patch pairs/replication) where each trapping occasion was sampled for 3 consecutive nights.


Traditional
Patch Burn
2 unburned
1 unburned
3 unburned
4 unburned
6 unburned
5 unburned
2 Fall Burn
1 Spring Burn
3 Spring Burn
4 Fall Burn
6 Fall Burn
5 Spring Burn
Year 1
Year 2
Year 3



1 Trap Occasion = 1 Patch Pair from each Replication

1 Sampling Period = 6 Trap Occasions (i.e. 1 trap occasion per patch pair)

Figure 2. Abundance (mean individual captures/100 trap nights) of 5 small mammal species on control (*n* = 3) and patch burn (*n* = 3) treatments. Numbers above bars represent total number of captures/100 trap nights within a given trap session.

Traditional ☐ Patch Burn ▨

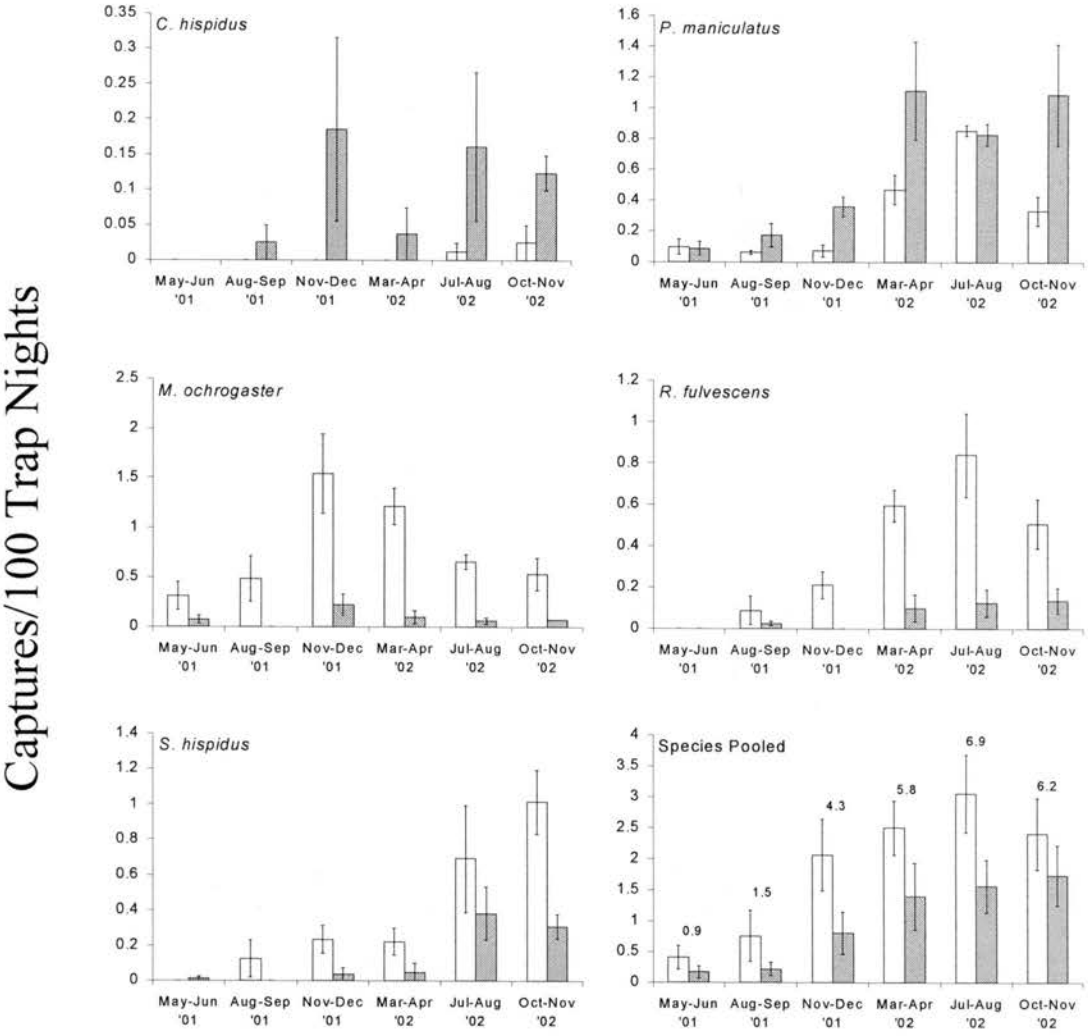
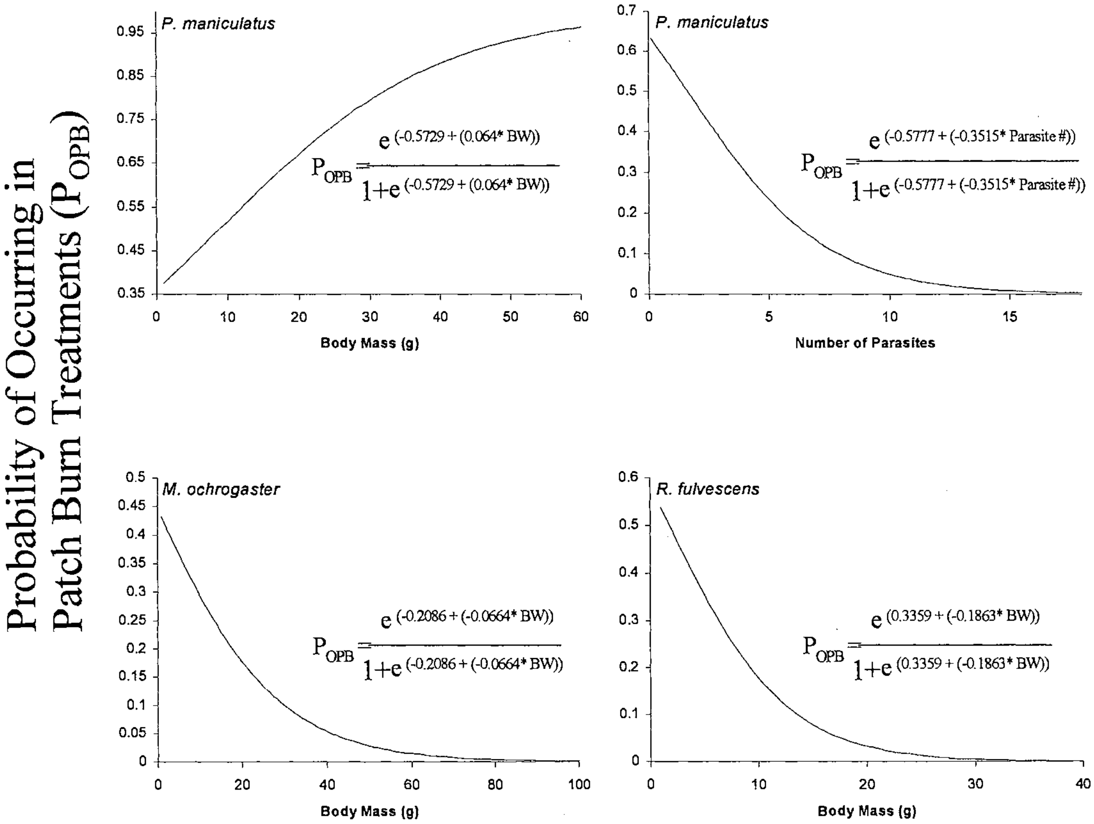

Captures/100 Trap Nights
C. hispidus
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
P. maniculatus
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
M. ochrogaster
2.5
2
1.5
1
0.5
0
R. fulvescens
1.2
1
0.8
0.6
0.4
0.2
0
S. hispidus
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Species Pooled
4
3.5
3
2.5
2
1.5
1
0.5
0
0.9
1.5
4.3
5.8
6.9
6.2
May-Jun '01
Aug-Sep '01
Nov-Dec '01
Mar-Apr '02
Jul-Aug '02
Oct-Nov '02

Figure 3. Relationships between body mass and parasite loads to the predicted probability of *P. maniculatus*, *M. ochrogaster*, and *R. fulvescens* occurring in patch burn treatments on the Oklahoma State University Range Research Station, Stillwater, Oklahoma, 2001 – 2002. Values calculated from probability equations derived from univariate logistic-regression models ($P < 0.05$).


Probability of Occurring in Patch Burn Treatments (P_{OPB})
P. maniculatus
$P_{OPB} = \frac{e^{(-0.5729 + (0.064*BW))}}{1+e^{(-0.5729 + (0.064*BW))}}$
0.35
0.45
0.55
0.65
0.75
0.85
0.95
0
10
20
30
40
50
60
Body Mass (g)
P. maniculatus
$P_{OPB} = \frac{e^{(-0.5777 + (-0.3515*Parasite\#))}}{1+e^{(-0.5777 + (-0.3515*Parasite\#))}}$
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0
5
10
15
Number of Parasites
M. ochrogaster
$P_{OPB} = \frac{e^{(-0.2086 + (-0.0664*BW))}}{1+e^{(-0.2086 + (-0.0664*BW))}}$
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0.45
0.5
0
20
40
60
80
100
Body Mass (g)
R. fulvescens
$P_{OPB} = \frac{e^{(0.3359 + (-0.1863*BW))}}{1+e^{(0.3359 + (-0.1863*BW))}}$
0
0.1
0.2
0.3
0.4
0.5
0.6
0
10
20
30
40
Body Mass (g)

CHAPTER 3

INFLUENCE OF GRAZING ON SPATIAL HETEROGENEITY OF SOIL-SURFACE TEMPERATURE

Abstract. While most studies of heterogeneity have focused on describing patterns of species or communities, few have focused on the relationships between biotic and abiotic environmental landscape-level gradients. Our study was designed to determine relationships between grazing (heavy, moderate, ungrazed), topographic position (upland vs riparian), vegetation structure, and the thermal environment (i.e. soil surface temperatures) and determine the influence on landscape patterns of heterogeneity. Biotic and abiotic patterns of heterogeneity were evaluated by establishing 200-m transects that were centered on and perpendicular to a riparian zone so that spatial patterns of variability could be determined along each transect which transcends the maximum level of landscape heterogeneity. Vegetation cover and structure and soil surface temperatures were recorded at 1-m intervals along the transect. Bare ground increased and leaf litter, grass cover, vegetation heights and angle of obstruction decreased with grazing intensity. However, mean soil surface temperatures did not differ between grazing treatments. Tree canopy cover associated with riparian areas generally reduced soil surface temperatures 20 °C below that of upland temperatures. In fact, 96% of observations of riparian soil-surface temperature were ≤ 39 °C, while 94% of upland soil surface temperatures were ≥ 40 °C regardless of grazing intensity. Vegetation characteristics and soil-surface temperatures were correlated, but correlation coefficients were small because soil-surface temperature was highly variable. Grazing influenced patterns of landscape heterogeneity, but effects were inconsistent among biotic and abiotic variables. Although grazing had little influence on moderating mean soil surface temperatures, results suggest that grazing intensity influences thermal heterogeneity at a variety of spatial scales. For instance, thermal heterogeneity (in moderately grazed treatments) is highest at smaller (lag distances ≤ 20 m) and larger (i.e. lag distances ≥ 48 m) spatial scales but was lowest at moderate scales (lag distances 22−45 m). For all variables, other than soil surface temperature and forb cover, semi-variances of moderately grazed sites generally lie intermediate between heavy and ungrazed sites. Nearly all ungrazed vegetation characteristics, except leaf litter, fit a spherical model that reached a sill at a lag distance ≤ 20 m and became spatially independent thereafter, while heavy and moderate grazed sites typically fit an exponential model, indicating a high degree of continuity. Patterns of thermal variability (on uplands) are not related directly to any one vegetational variable, hence, landscape patterns based on vegetational parameters alone are of limited value since patterns of thermal variability are effected by the integration of vegetational and environmental variables within the ecosystem.

Keywords: *Disturbance, Grazing, Mixed Grass Prairie, Habitat, Spatial Dependence, Temperature, Vegetation Structure.*

Nomenclature: Hatch et al. (1990)

INTRODUCTION

Many ecologists are beginning to recognize the role of heterogeneity in ecological systems by acknowledging its influence on population dynamics and biodiversity (MacArthur and Pianka 1966, Wiens, 1976, Turner and Gardner 1991, Sarnelle et al. 1993). In fact, it has been suggested that heterogeneity is actually the root of biological diversity at all levels of ecological organization and should serve as the foundation for conservation and ecosystem management (Christensen 1997, Ostfeld et al. 1997, Wiens 1997). Concern regarding the role of spatial heterogeneity in influencing population and community dynamics had gained recent attention (Levin 1992, Wiens 1997, White and Walker 1997, Sanderson and Harris 2000, Fuhlendorf and Engle 2001). Spatially discrete disturbance patterns were described historically as a shifting mosaic (Kay 1998, Fuhlendorf and Engle 2001), where the presence of alternative habitat types may have provided 1) complementary resources (i.e. food availability, cover from predators or climate) that improved habitat quality for some species and/or 2) provided unique habitat types capable of supporting a variety of species, both of which presumably enhance biodiversity. Because heterogeneity is largely associated with spatial and temporal variability, it is highly scale dependent and can be influenced by many factors including grazing and topo-edaphic features (Fuhlendorf and Smeins 1996, 1999).

Increasing evidence suggests that specific microclimates within a species' range can have profound effects on population dynamics (survival, movements, fitness) and may dictate habitat utilization throughout the year (Sedgeley 2001, Sharp and Van Horne 1999). The influence of temperature on the biotic community has been widely documented (Loik et al. 2000, Roads et al. 1994, Daubenmire 1974), but landscape temperature patterns are reported rarely in ecological studies (Chen et al. 1996). Thermal properties are critical aspects of animal survival throughout the summer months. To maintain body temperature, animals must balance heat gained from the environment by heat loss to the environment. Metabolic rates required to maintain body temperatures are influenced positively by the gradient between body and ambient temperature (Ricklefs 1976). Thus, animals are forced to entertain tradeoff decisions between foraging behavior, predator avoidance, and thermal refuge. To tolerate such extremely high temperatures, plants and animals must adapt physiologically, morphologically and/or behaviorally to their thermal environments (Calder and King 1974, Jones 1983). Animals that efficiently utilize microhabitats to conserve energy may gain an advantage by reallocating these reserves to other vital processes (Walsberg 1985, 1986, 1993, Webb and Rogers 1988).

Although vegetation characteristics (i.e. availability and distribution of food, structure and cover) dictate habitat selection for many wildlife species (Ostfeld 1985, Kendeigh and Fawver 1981, Pierson and Wight 1991), they also are a critical moderator of local temperatures (Pianka 1988). Further, livestock grazing may be the most influential process governing changes in vegetation structure and composition (Holechek et al. 1989, Milchunas and Lauenroth 1993). Thus, direct and indirect influences of temperature and livestock grazing can have an influence on ecosystem function by influencing distribution and abundance of a wide range of animal species including insects, birds and mammals (Bock et al. 1984, Dennis et al. 1998, Ritchie 2000). For instance, interactions between air temperature and livestock grazing can influence soil moisture, photosynthetic, respiration and decomposition rates creating unique habitat types that ultimately influence distribution and abundance of plant and animal populations (Geiger 1965, Daniel et al. 1979, Perry 1994). Consequently, distribution of landscape level temperature gradients may have profound effects on distribution and abundance of biological communities, especially those occupying hot arid environments (Schleucher 1999, Karr and Freemark 1983). Hence, moderation of the thermal environment is a critical abiotic factor and landscape function governing all life processes and should be considered as an important factor in community ecology.

As levels of atmospheric CO_2 continue to increase (Keeling et al. 1995), debates about the influence of elevated atmospheric CO_2 and global temperature have gained recent attention and will likely continue in the foreseeable future. However, there is no debate regarding the ability of temperature to dictate distribution and abundance of biotic communities (Risklefs 1976, Calder and King 1974, Jones 1983, Walsberg 1993). Thus, quantifying relationships between landscapes and the thermal environment will likely play an increasing role in conservation and restoration of many ecological systems. Our study site provided us an excellent opportunity to examine relationships between soil surface temperature, vegetation and grazing on patterns of landscape heterogeneity. Our site is located within the Southern Great Plains of North America where extremely high air temperatures ($\bar{x} = 37$ °C) and livestock grazing are common throughout the summer months.

Although habitat selection is generally described by quantifying vegetation characteristics (i.e. % cover, structure, species composition) within a species home range, other potentially important habitat features such as soil moisture (Kendeigh and Fawver 1981) and temperature (Pierson and Wight 1991) should be further evaluated as key indicators of site selection for many biological organisms. It is unclear how patterns of soil-surface temperature might influence distribution and abundance of plant and animal populations. To better understand the ecological importance of these relationships to conservation and restoration of our native ecosystems, we designed an experiment to document relationships between thermal patterns of landscape variability and vegetation characteristics associated with livestock grazing. We hypothesized that soil-surface temperatures and heterogeneity would be influenced strongly by patterns of vegetation and grazing intensity.

MATERIALS AND METHODS

Study Area

The study area was located approximately 15 km south of Clinton, Oklahoma in the Rolling Red Plains Resource Area of the southern Great Plains. Average annual precipitation was 77 cm and ranged from 51 to 82 cm (Fuhlendorf et al. 2001). Approximately 70% of the rainfall occured during the primary growing season from April to September. The 600-ha research station was largely rolling uplands cut by several steep drainages with a mean elevation of 490 m. Rock outcrops and bare areas were common. Soils were highly erosive and primarily classified as a Cordell silty clay loam with a depth of 25 to 36 cm over solid siltstone (Moffatt and Conradii 1979, Fuhlendorf et al. 2001). The vegetation was typical of the mixed-grass prairie with variable dominant species dependent upon topo-edaphic effects and land use. On uplands the dominant species were a mixture of grasses with variable stature. Dominant mid-grasses included *Bouteloua curtipendula*, *Aristida purpurea*, and *Bothriochloa saccharoides*. Short grasses were more abundant with shallow soils or heavy grazing and include *Bouteloua gracilis*, *Buchloe dactyloides*, and *Bouteloua hirsuta*. Tallgrasses were less abundant and restricted to protected mesic sites but include *Schizachyrium scoparium*, *Sorghastrum nutans* and *Andropogon gerardii*. There also was a high diversity of herbaceous dicots that varied with annual fluctuations in precipitation. Woody plant species include *Rhus glabra* and *Prunus angustifolia* in isolated portions of the landscape, as well as the widely distributed sub-shrub, *Guiterrezia sarothrae*. Riparian zones made up < 5% of the total area and are dominated by *Populus deltoides*, *Ulmus americana*, *Bumelia lanuginosa*, and *Sapindus Drummondii* (Fuhlendorf et al. 2001). Taxonomic nomenclature follows Hatch et al. 1990.

Methods

Replicated treatments were established on ca. 45 ha that were subjected to heavy (n = 2), moderate (n = 2), and ungrazed (n = 2) treatments to determine associations between soil surface temperature and grazing. Heavy and moderate grazed sites were stocked with stocker cattle ($\bar{x}$ = 270 kg) at 2 ha/animal and 3.75 ha/animal, respectively, from 1 April to 31 September. We established 200-m transects in each replication (n = 6) that were centered on and ran perpendicular through a riparian zone so that the effects of topographic position (upland, riparian) and spatial patterns of variability would be maximized for each transect. We used a 0.25-m^2 quadrat to characterize plant cover and soil surface temperatures at 1-m intervals along the transect. Estimates of percent cover by plant functional group (grass, forb, shrub, litter and bare ground) were recorded using the mid-point of the following cover classes of 0–5, 6–25, 26–50, 51–75, 76–95, and 96–100% (Daubenmire 1959). Tree canopy cover within the riparian area was dominated by *Populus deltoides* and *Ulmus americana* and generally covered all plots within the riparian area. Soil-surface temperatures were recorded during the period of greatest physiological stress (August) for plant and animal communities in this region. We restricted collection times between 1100 and 1700 hours when air temperature and light intensity were maximized (i.e. 0% cloud cover). Air temperature and solar radiation ranged from 36.3–37.3 °C and 733–894 watts/m^2, respectively, during our collection times. Soil surface temperatures were recorded using an OMEGASCOPE OS531 hand held infra-red thermometer (One Omega Drive, Box 4047 Stamford, CT 06907). Temperature measurements were intended to represent the conditions important to ground-level organisms and were obtained by placing the thermometer ca. 3 cm above the surface of the ground. Soil surface temperatures are defined as that layer of material between the thermometer and the ground surface but could include bare soil, rock, leaf litter or herbaceous material at the soil surface. We recorded 5 soil-surface temperatures: 4 at 6 cm from each quadrat corner and 1 directly in the center. To quantify relationships between vegetation structure and soil-surface temperatures, we also recorded the maximum plant vegetation height from the center of each quadrat and determined the angle of obstruction along 8 radii at 45° compass intervals to quantify vertical and horizontal vegetation structure, an important indicator of ground nesting bird habitat (Kopp et al. 1998, Harrell and Fuhlendorf 2002). All upland measurements were recorded on slopes <

3° and slopes along the upland-riparian edge were generally < 5° with an east-west orientation.

Statistical Analyses

We compared percent cover of plant functional groups between grazing treatments (heavy, moderate, and ungrazed) and landscape position (riparian, upland) using PROC ANOVA (SAS Institute Inc. 1999). Interactions were not significant ($P > 0.05$) so sources of variation were distributed among main factor effects (grazing treatment and landscape position). To assess the influence of vegetation cover variables on temperature, we used stepwise regression analysis (PROC REG; SAS Institute, Inc. 1999), with temperature as the dependent variable and cover of plant functional groups as the independent variables. Variables selected for inclusion in the model were significant when $P \leq 0.15$ (Hosmer and Lemeshow 1989, Sams et al. 1996, Cody and Smith 1997). The suitability of this model was tested using the Hosmer-Lemeshow goodness-of-fit statistic at $P > 0.05$ (Hosmer and Lemeshow 1989). We also examined relationships between cover of plant functional groups and temperature using Pearson correlation analysis (PROC CORR, SAS Institute Inc. 1996).

To determine spatial patterns of temperature along the line, we calculated semi-variograms to characterize spatial patterns of soil surface temperatures within each grazing treatment (Clark 1980, Turner et al. 1991). The semi-variance is the sum of squared differences between all possible pairs of points separated by a particular distance, typically where measurements are uniformly spaced along a straight line (Turner et al 1991). Semi-variograms are defined by (1) the *sill*, which is the horizontal portion of the graph where the semi-variance tends to level off at the maximum semivariance, (2) the *range of influence* is determined by the lag distance associated with the sill (commonly referred to as patch size), where points farther apart than the range are independent (because at distances greater than the range the semivariance equals the sample variance) and points closer than the range bear some relationship to one another, and (3) the *nugget* or y-intercept, which represents sampling error or variability occurring at scales smaller than the sampling interval (Clark 1980). Semi-variograms typically fit 4 types of theoretical models (linear, gaussian, exponential and spherical) used to interpret spatial data (Fig 1). A flat variogram, also called the 'nugget effect', indicates random variation, where all measurements along the line are unrelated to one another, implying zero spatial correlation (Trangmar et al. 1985).

RESULTS

Grazing altered the composition and cover of these grassland ecosystems. Amount of bare ground increased with grazing and was 3-fold greater in heavy than in ungrazed pastures (Table 1). In contrast, leaf litter decreased with grazing intensity and was nearly 10-fold greater in ungrazed sites (Table 1). Cover of grass was higher in ungrazed than in heavy grazed sites, but there was no difference in forb or shrub cover between grazing treatments (Table 1). Vegetation height and angle of obstruction were greatest in ungrazed sites and decreased with grazing intensity (Table 1).

Mean soil-surface temperatures did not differ between grazing treatments. As a result, data were pooled across treatments to evaluate differences between landscape positions (upland and riparian). Analysis of variance showed that upland (n = 1045, $\bar{x}$ = 51 °C, *c.v.* = 14.51) soil surface temperatures were greater ($P < 0.001$) than those within the riparian area (n = 155, $\bar{x}$ = 30°C, *c.v* = 22.78; Fig. 2). Only 6% of upland vs. 96% of riparian soil surface temperatures were < 40 °C (Table 2).

Best-fit multiple regression models that predicted soil-surface temperature from vegetation characteristics within the riparian ($R^2 = 0.09$ $F = 2.43$, $P = 0.121$, 2 variable model) and uplands ($R^2 = 0.22$, $F = 12.27$, $P = 0.001$, 3 variable model) explained only a small percentages of variation in soil-surface temperature (Table 3). The significance of the upland model was largely due to the large sample size (n = 1045). On uplands, bare ground was the best predictive variable accounting for only 12% of the variation in soil-surface temperature (Table 3), where increases in bare ground and leaf litter were associated positively with temperature (Fig. 3). Cover of grass and vegetation height were correlated negatively with soil surface temperature (Fig 3). Although significant correlations existed between community parameters (bare ground, cover of leaf litter, cover of grass and vegetation height) and soil surface temperature, all correlation coefficients were small ($r < 0.34$, Fig 3).

Standard deviations in soil-surface temperatures were greater between quadrat averages than within quadrats for both upland and riparian sites. Upland standard deviations between quadrat averages ranged from 7.1 to 8.0 °C across all grazing treatments. Within the riparian zone, the highest variability occurred in the moderate grazed treatment followed by ungrazed and heavy grazed treatments (Table 4). Standard deviations of soil surface temperatures within 0.25-m^2 quadrats were similar across all upland grazing treatments and averaged about 4 °C, while riparian standard deviations within 0.25-m^2 quadrats ranged from 1 to 2 °C (Table 4). However, some 0.25-m^2 quadrats had individual temperatures that varied by as much as 34 °C. Standard deviations in soil-surface temperature within quadrats were 1.9 to 3.5 times greater on uplands than within riparian zones (Table 4).

Mean widths of the riparian zone was similar for heavy (33 m), moderate (36 m), and ungrazed (28 m) treatments and allowed us to make direct semi-variance comparisons between treatments. The form of the semi-variogram based on soil-surface temperature was rather unique compared with semi-variograms based on vegetation characteristics. Semi-variance of soil-surface temperature was spatially dependent and rose continuously with lag-distance in heavy and ungrazed pastures, indicating a high degree of continuity (i.e. exponential model; Fig 4). However, moderately grazed treatments also were spatially dependent, but the relationship was spherical, indicating that moderately grazed sites had a higher degree of landscape variability than other grazing treatments (i.e. points > 16 m are unrelated or independent of one another; Fig 4). For example, semi- variance of 250γ occurred at 8 m in moderately grazed sites vs. 16 m in heavy and un-grazed sites, indicating that moderately grazed treatments exhibited a higher degree of thermal heterogeneity at the landscape level (Fig. 4).

For all variables other than soil surface temperature and forb cover, semi-variances of moderately grazed treatments lie intermediate between heavy and ungrazed sites (Fig 4).

Semi-variance of heavy grazed sites were primarily lower for most vegetation characteristics, while ungrazed sites were typically higher than moderately grazed sites. However, these semi-variance relationships between heavy and ungrazed sites were inversed for cover of bare ground and angle of obstruction (Fig 4). Nearly all ungrazed vegetation characteristics, except leaf litter, fit a spherical model that reached a sill at a lag distance ≤ 20 m and became spatially independent thereafter, while heavy and moderate grazed sites typically fit an exponential model that never reached a sill, indicating that ungrazed treatments were more heterogenous than heavy or moderately grazed treatments.

DISCUSSION

Relationships between vegetation and temperature

Significant variations in soil heat flux can occur in regions where vegetation cover is clumped with large areas of exposed soil (conditions that are common on our upland study sites) and temperature variability is highest during the mid-afternoon hours (Kustas et al 2000, Saunders et al. 1998). Therefore, it was reasonable to expect landscape soil surface temperatures to be highly variable across multiple spatial scales on our study site. My study suggests that within a very small area ($< 0.25\text{-m}^2$) temperatures can vary from biologically tolerable (typically < 40°C) to extremely hot and potentially lethal (≥ 50°C). Temperatures ≥ 50°C are capable of destroying vital proteins that are essential for life support (Calder and King 1974, Daubenmire 1974, Larcher 1991). Hence, thermal patterns of landscape variability may be a critical habitat feature capable of limiting the distribution and abundance of plant and animal species throughout the day, especially in hot arid environments.

Further, it is likely that available habitat determined by the thermal environment will vary temporally throughout the day as the angle of sun rays change with respect to the landscape variables (i.e. vegetation structure, slope, aspects etc. that intercept sun rays) and seasonally throughout the year. Thus, consideration of landscape-level thermal patterns may be a critical component to understanding ecological processes associated with biodiversity and conservation at multiple spatial and temporal scales.

On our study site, riparian drainages were typically covered (> 50%) with an overstory of deciduous trees. Because canopy shading from trees reduces the amount of solar radiation at the soil surface (Larcher 1991), we expected landscape position to have an influence on soil-surface temperatures. On our study site, topographic position may be the most important factor moderating mean soil-surface temperature. For instance, soil-surface temperatures in wooded riparian areas were on average 20 °C below that of upland temperatures. In fact, 96% of all riparian soil-surface temperatures were ≤ 39 °C, while 94% of upland soil surface temperatures were ≥ 40 °C during the heat of the day. This temperature pattern between open and closed canopies also has been documented along forest edges (Didham and Lawton 1999). Under a canopy of trees, the flux of thermal energy is greatly reduced, so that within the riparian zone soil-surface temperatures are less variable over space during extremely hot conditions (Larcher 1991). As a result, the degree to which the riparian-upland edge influenced soil-surface temperatures indicates that habitats capable of supporting thermally tolerable temperatures may be drastically reduced on upland sites during the heat of the day. Although riparian habitats are a minor component of these landscapes (<5%), they may be a critical habitat component to many animals during the heat of the day.

Cover of vegetation < 0.5 m tall is generally a poor predictor of soil-surface temperature; vegetation heights > 0.5 m are most important (Saunders et al. 1998). To document relationships between structural differences in vegetation and mean soil-surface temperature throughout the landscape, we chose only to analyze upland sites (vegetation cover typically < 0.5 m tall) because of the obvious overriding effect of canopy shading (i.e. shrubs and trees > 0.5 m tall) in the riparian areas. In general, vegetation characteristics on uplands were poor predictors of soil-surface temperature. Bare ground was the best predictive variable but accounted for only 12% of the variation in soil-surface temperature. On the uplands, cover of grass and vegetation height was related inversely to soil-surface temperatures, while bare ground and leaf litter were associated positively with soil-surface temperature. The positive association between leaf litter and soil-surface temperatures may seem counterintuitive but likely is related to the proportion of cover that is transpiring plant material. For instance, in heavy grazed sites the interstitial spaces between clumps of vegetation cover is primarily composed of bare ground, which can increase temperatures. However, as grazing intensity decreases, bare soil is replaced progressively by leaf litter. So depending on grazing intensity, bare ground or litter is an indication of the absence of live transpiring plants. Because, controlling the rate of transpiration through stomatal regulation is an efficient technique that acts to cool the plant and the surrounding environment (Daubenmire 1974, Larcher 1991), the temperature response to cover of leaf litter and bare ground was similar, presumably because the cover of transpiring plants (grasses, forbs, and shrubs) generally did not differ between treatments (Table 1). Further, the semivariances of temperature (350γ) and leaf litter (600γ) within moderately grazed sites support our conclusions because they both correspond to a patch size of ca. 16 m, indicating that they may be spatially related.

Influence of grazing on heterogeneity

Many studies have documented the effects of grazing intensity on vegetation structure (Dyksterhuis 1949, Ellison 1960, Fuhlendorf and Smeins 1997), and variables associated with vegetation or ground cover can explain differences in soil-surface temperatures in some ecosystems (Saunders et al. 1998), so we predicted that vegetation patterns and mean soil- surface temperatures would be influenced by grazing intensity. Surprisingly, the variability in soil-surface temperature, on our study site, was similar across all grazing treatments, implying that grazing intensity had little influence on moderating soil surface temperatures under these severe conditions.

Because animals selectively graze at multiple scales and because they do not graze uniformly (Senft et al. 1987), grazing is likely to have an influence on the spatial arrangement of vegetation (Fuhlendorf and Smeins 1997, 1998). On our study site, grazing appears to have a predictable influence on the pattern of nearly all vegetation variables throughout the landscape. For example, semi-variances of variables within moderate grazed sites, with the exception of forb cover, consistently lie intermediate between heavy and ungrazed sites, suggesting that moderately grazed sites exhibit patterns associated with moderate levels of semi-variance. Our results demonstrate that thermal heterogeneity was greatest within moderately grazed treatments, yet heterogeneity of vegetation (i.e. litter, grass, forb, shrub cover, and vegetation height) was greater in ungrazed treatments than in treatments that were heavily or moderately grazed. However, semi-variances of bare ground and angle of obstruction was greatest within heavy grazed and lowest in ungrazed sites, with a range of ≤ 15 m, suggesting that these patterns of variability changed ca. every 15 m across the landscape. The average range (lag distance) and semi-variance associated with all vegetation characteristics differed with grazing treatment. Most vegetation characteristics within moderate and heavy grazed sites typically fit an exponential model that never reached an obvious sill (Fig. 3), indicating that patterns of heterogeneity are not apparent or occur on those sites at larger spatial scales (i.e. ≥ 50 m).

Grazing can increase, decrease or have no effect on spatial heterogeneity (McNaughton 1984, Adler and Lauenroth 2000, Fuhlendorf and Smeins 1999). Our results clearly supported these conclusions and demonstrated that grazing can impose distinct patterns of heterogeneity on both biotic and abiotic ecosystem components, but patterns of heterogeneity were not consistent and depended on the variable of interest and spatial scale. For instance, variability of ungrazed sites were highly dependent on the variable of interest, where variability of biotic components (i.e. cover of leaf litter, forbs, and shrubs) was highest across all spatial scales, but variability of bare ground and angles of obstruction was lowest at all scales of observation. In contrast, influences of grazing on thermal heterogeneity (in moderately grazed treatments) were highest at smaller (i.e. lag distances ≤ 20 m) and larger (i.e. lag distances ≥ 48 m) spatial scales and were lowest at moderate scales (lag distances 22 – 45 m). Thus, our data leaves little doubt that grazing can reduce and/or increase the inherent variability in vegetation that is created by environmental variables (e.g. soil type, moisture, topography, etc.) and that the range of influence across ecological systems is highly scale dependent (Glenn et al. 1992, Adler and Lauenroth 2000). These findings are consistent with previous reports from the shortgrass steppe (Milchunas et al. 1989, Milchunas and Lauenroth 1989), tallgrass prairie (Glenn et al. 1992) and mixed grass savanna (Fuhlendorf and Smeins 1998, 1999), where increases in grazing intensity were associated positively and/or negatively with heterogeneity.

CONCLUSIONS

Most previous studies of landscape heterogeneity have focused on variability of vegetation components with clear discontinuities that are often created by soil, topographic variation or disturbances associated with vegetation. But, relationships between vegetation structure, topographic position, grazing, and microclimate act in concert to shape grassland ecosystems and habitats. On our study site, effects of grazing on landscape heterogeneity are highly variable and depend primarily on the variable of interest and scale of observation. Further, presumably because soil surface temperatures were highly variable within a relatively small area (i.e. ≤ 0.25 m^2), grazing did not influence mean soil surface temperature and results suggested that landscape position was the most important component moderating mean soil surface temperatures. Lower soil surface temperatures (associated with riparian areas) may provide a critical thermal refuge for many animals on hot summer days when air temperatures can exceed 37 °C. Patterns of thermal heterogeneity were not directly related to any one vegetation variable, hence, landscape patterns based on vegetation parameters alone, are limited in their use since patterns of thermal variability are likely influenced by the integration of vegetation and environmental variables. We recommend that ecologists who are interested in conservation or restoration evaluate biotic ecosystem components while simultaneously considering abiotic components.

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Table 1. A comparison of vegetation characteristics (percent ground cover, vegetation height, and angle of obstruction) between grazing treatments on Marvin Klemme Range Research Station, Bessie, Oklahoma, 2000.

	Heavy^{a,b}			Moderate^{c}			Ungrazed		
Vegetation characteristic	*n*	$\bar{x}$	*SD*	*n*	$\bar{x}$	*SD*	*n*	$\bar{x}$	*SD*
Bare ground	398	$36^{***,***}$	32.4	400	23^{***}	30.1	399	12	23.7
Leaf litter	398	$2^{***,***}$	10.4	400	10^{***}	24.6	399	19	31.5
Grass	398	$51^{ns,*}$	34.4	400	54^{ns}	34.4	399	57	38.5
Forb	398	$24^{ns,ns}$	22.8	400	25^{ns}	22.4	399	27	25.9
Shrub	398	$3^{ns,ns}$	14.5	400	3^{ns}	15.5	399	2	13.9
Vegetation height (cm)	400	$28^{***,***}$	22.6	400	37^{***}	31.9	400	53	36.0
Angle of obstruction (°)	400	$46^{***,**}$	37.3	400	53^{***}	36.5	400	73	29.7

Significance indicated by: ^{ns} = nonsignificant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
[a] ANOVA test for heavy vs. moderate treatments.
[b] ANOVA test for heavy vs. ungrazed treatments.
[c] ANOVA test for moderate vs. ungrazed treatments.

Table 2. Frequency and percent of soil surface temperatures collected along 200 m transects on Marvin Klemme Range Research Station, Bessie, Oklahoma during summer 2000.

	Upland		Riparian		Pooled	
Temperature °C	*n*	%	*n*	%	*n*	%
0–39	66	6.3	148	95.5	214	17.8
40–59	859	82.2	6	3.9	865	72.1
> 60	120	11.5	1	0.7	121	10.1

Table 3. Vegetation characteristics (cover of plant functional groups, angle of obstruction, and vegetation height) selected by a stepwise multiple regression analysis to predict soil surface temperatures on Marvin Klemme Range Research Station, Bessie, Oklahoma, 2000.

Landscape Position	Variable	Parameter Estimate	*SE*	Partial R^2	*F*	*P*
Upland	Intercept	49.12	0.51	–	9165.48	<0.001
	Bare ground	0.10	0.01	0.12	126.01	<0.001
	Litter	0.13	0.01	0.09	113.35	<0.001
	Height	−0.03	0.01	0.01	12.27	0.001
Riparian	Intercept	28.06	0.70	–	1604.46	<0.001
	Grass	0.03	0.02	0.07	3.79	0.054
	Angle of obstruction	0.02	0.02	0.02	2.43	0.121

Table 4. Mean soil-surface temperature (°C), standard deviation (SD), and coefficient of variation (CV) for different grazing intensities and topographic positions (between quadrats and within quadrat), along 200 m transects on Marvin Klemme Range Research Station, Bessie, Oklahoma, summer 2000.

	Heavy				Moderate				Ungrazed			
Topographic Position Scale	*n*	$\bar{X}$	*SD*	*CV*	*n*	$\bar{X}$	*SD*	*CV*	*n*	$\bar{X}$	*SD*	*CV*
Upland												
Within quadrat	1765	51	4.32	8.56	1735	50	4.41	8.74	1725	52	4.30	8.17
Between quadrats	353	51	7.95	15.57	347	50	7.09	14.12	345	52	7.08	13.61
Riparian												
Within quadrat	235	29	1.23	4.12	265	29	2.21	7.52	275	31	1.42	4.61
Between quadrats	47	29	3.91	13.27	53	29	8.59	30.02	55	31	6.62	21.28

Fig. 1. Four of the most common theoretical semi-variogram models (Isaaks and Srivastava 1989).

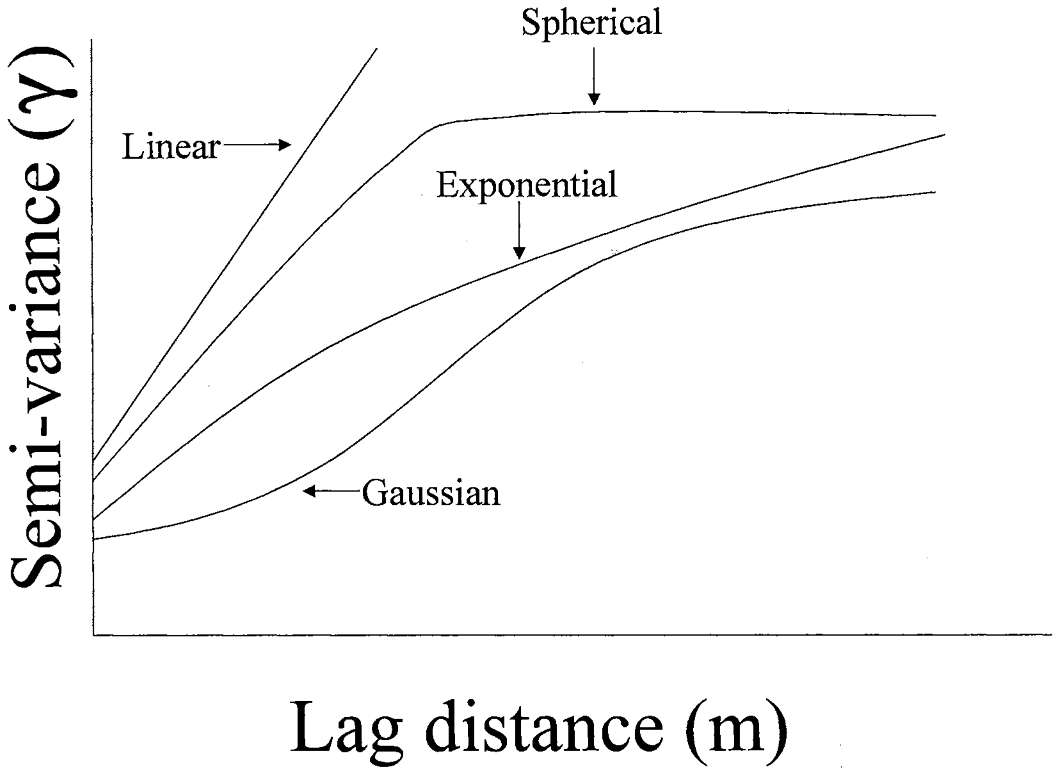
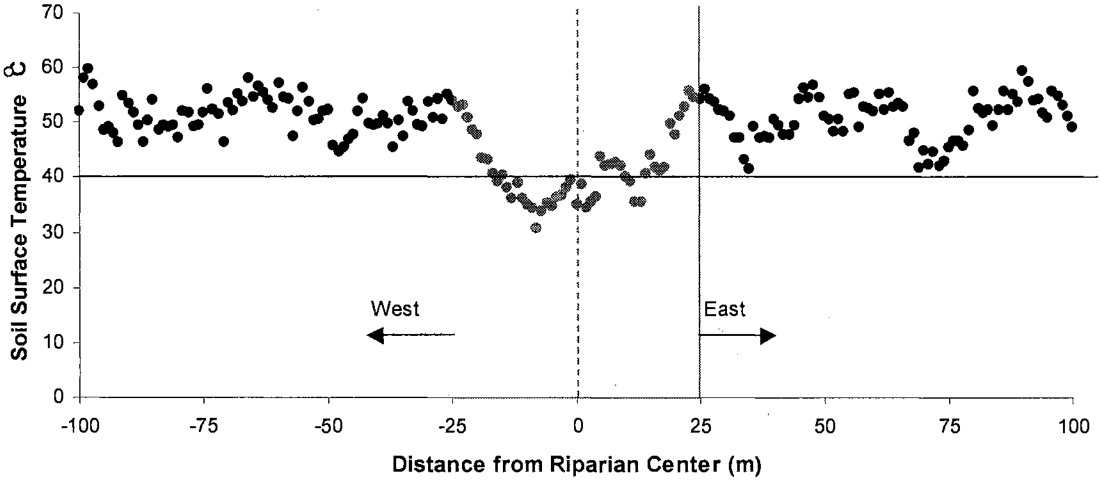

Spherical
Linear
Exponential
Gaussian
Semi-variance (γ)
Lag distance (m)

Fig. 2. Mean east-west soil surface temperature (°C) gradient pooled across grazing treatments (heavy, moderate, and ungrazed) on Marvin Klemme Range Research Station, Bessie, Oklahoma, 2000. The center of the riparian zone lies at 0 m, and the mean structural edge between riparian and upland areas lies at ±25 m.



70
60
50
40
30
20
10
0
Soil Surface Temperature °C
West
East
-100
-75
-50
-25
0
25
50
75
100
Distance from Riparian Center (m)

Fig. 3. Correlation coefficients describing relationships between vegetation cover on uplands and soil surface temperatures on Marvin Klemme Range Research Station, Bessie, Oklahoma, 2000. Because we used the midpoint associated with Daubenmire's cover classes, we plotted the mean and standard error of soil surface temperatures associated with each midpoint cover class. All points associated with vegetation height were plotted against soil surface temperatures because vegetation heights were associated with continuous rather than categorical data.

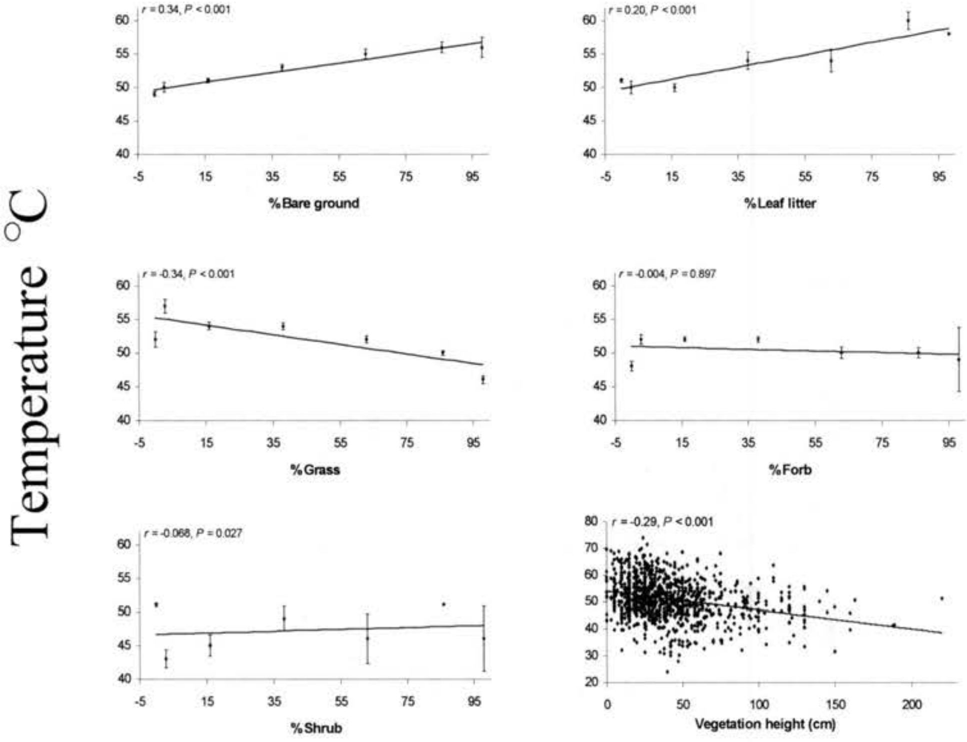
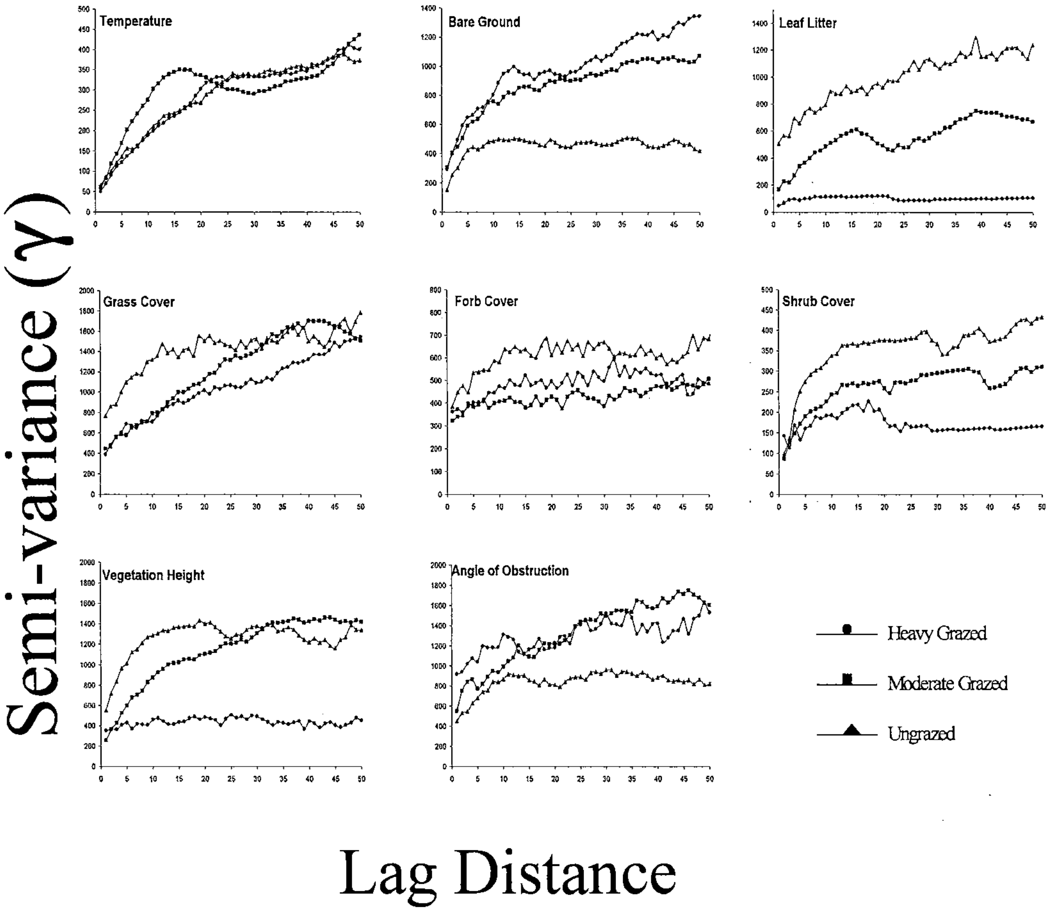

Temperature °C
r = 0.34, P < 0.001
%Bare ground
r = 0.20, P < 0.001
%Leaf litter
r = -0.34, P < 0.001
%Grass
r = -0.004, P = 0.897
%Forb
r = -0.068, P = 0.027
%Shrub
r = -0.29, P < 0.001
Vegetation height (cm)
40
45
50
55
60
-5
15
35
55
75
95
20
30
70
80
0
100
150
200

Fig. 4. Semi-variograms based on vegetation characteristics and soil surface temperatures for heavy, moderate, and ungrazed treatments during August on Marvin Klemme Range Research Station, Bessie, Oklahoma, 2000.


Temperature
Bare Ground
Leaf Litter
Grass Cover
Forb Cover
Shrub Cover
Vegetation Height
Angle of Obstruction
Heavy Grazed
Moderate Grazed
Ungrazed
Semi-variance (γ)
Lag Distance

CHAPTER 4

ARTIFICIAL NEST SUCCESS IN MIXED-GRASS PRAIRIE: IMPACTS OF GRAZING AND TOPOGRAPHIC POSITION

Abstract: Nest predation has been documented widely as a primary cause of avian reproductive failure and is an important factor limiting reproduction of many ground-nesting species. Because 70% of grassland bird species native to the North American Great Plains are in decline and most grasslands are managed for livestock grazing, its is essential to understand cause-effect relationships between grazing, vegetation patterns, and nest success. We used artificial nests to test relationships between artificial nest success and vegetation structure and cover as influenced by livestock grazing intensity within mixed-grass prairie habitat. Total predation on all nests exposed during the entire study period increased from 22% after 7 days to 52% after 23 days of exposure. Cover of plant functional groups and angle of obstruction progressively decreased with livestock grazing intensity and were generally greater on bottomlands. Predator response to artificial nests was not independent of spatial scale. Local variation in vegetation cover variables did not differ between successful and depredated nests after 7 or 23 days exposure. At larger spatial scale, predator response to artificial nests varied according to grazing treatment and landscape position, where rates of predation were less than expected only on sites that maximized vegetation cover (i.e. ungrazed bottomlands).

Key words: avian, birds, grasslands, habitat, scale, vegetation structure.

Introduction

Numerous studies have shown that some ground nesting grassland species select nesting habitats associated with a standing crop of old-growth vegetation. Livestock grazing may be the most influential process governing changes in habitat structure that ultimately influences nest site selection (Holechek et al. 1989). Grazing induced changes in vegetation components such as vegetation cover and structure and plant species composition can have a dramatic influence on the distribution and abundance of avian species (Ryder 1980, Bock et al. 1993), and a few studies have documented effects on nesting success of select species (Barker et al. 1990, Bowen and Kruse 1993).

Nest predation has been widely documented as a primary cause of avian reproductive failure and is an important factor limiting reproduction and population viability of many ground nesting species (Nice 1957; Nolan 1963, Ricklefs 1969, Nilsson 1984). However, nest predation rates are known to vary widely between species (Ricklefs 1969, Nilsson 1984) and among habitat types (Loiselle and Hoppes 1983, Savidge 1987). Differences in site selection (between species) and changes in vegetation pattern and structure (between habitats), presumably are responsible for the wide variation in reported rates of predation. Some grassland birds select nest sites associated with a high percentage of vegetation cover, presumably, because those sites provide concealment from predators and likely increases successful reproduction (Ricklefs 1969, Martin 1992). However, other birds select sites that are sparsely covered with vegetation, suggesting that predation may not be the driving factor associated with nest-site selection. Because 70% of grassland bird species native to the North American Great Plains are declining at a faster rate than any other guild in North America (Knopf 1994) and most grasslands are managed for livestock grazing, it is essential (for proper management of declining species) to understand cause-effect relationships between grazing, vegetation patterns and nest success.

To test these relationships, we used artificial nests to conduct a controlled experiment among replicated sites and treatments. Previous artificial nesting studies have used nest sites that are designed to simulate real nests by concealing eggs within dense vegetation in an attempt to estimate natural mortality rates. Because of documented concerns about using artificial nests to estimate natural mortality (Sugden and Beyersbergen 1986, Roper 1992, Haskell 1995), it is important to note that our objective was not to estimate predation rates of actual nests but was to determine the effects of grazing and landscape position on the probability of nest predation. When used in this context, artificial nests are a valuable tool in evaluating associations between vegetation patterns and artificial nest success. Our specific objectives were to test relationships between artificial nest success and vegetation structure and cover as influenced by grazing intensity within mixed grass prairie habitat of the North American great plains.

Study area and methods

Study Area

The area was located approximately 15 km south of Clinton, Oklahoma in the Rolling Red Plains Resource Area of the southern Great Plains. Average annual precipitation was 76.6 cm, ranging from 51.0 to 81.7 cm (Fuhlendorf et al. 2002). Approximately 70% of the rainfall occurred during the primary growing season from April to September. The 600-ha research station was largely rolling uplands cut by several steep drainages with a mean elevation of 490 m. Rock outcrops and bare areas were common. Soils were highly erosive and primarily classified as a Cordell silty clay loam with a depth of

25 to 36 cm over solid siltstone (Moffatt and Conradii 1979, Fuhlendorf et al. 2002). The vegetation was typical of the mixed-grass prairie with variable dominant species dependent upon topoedaphic effects and land use. On uplands the dominant species were a mixture of grasses with variable statures. Dominant mid-grasses include *Bouteloua curtipendula*, *Aristida purpurea*, and *Bothriochloa saccharoides*. Short grasses were more abundant with shallow soils or heavy grazing and include *Bouteloua gracilis*, *Buchloe dactyloides*, and *Bouteloua hirsuta*. Tallgrasses were less abundant and restricted to protected mesic sites but included *Schizachyrium scoparium*, *Sorghastrum nutans* and *Andropogon gerardii*. There also was a high diversity of herbaceous dicots that varied with annual fluctuations in precipitation. Woody plant species included *Rhus glabra* and *Prunus angustifolia* in isolated portions of the landscape, as well as the widely distributed sub-shrub, *Guiterrezia sarothrae*. Riparian zones made up less than 5% of the total area and were dominated by *Populus deltoides*, *Ulmus americana*, *Bumelia lanuginosa*, and *Sapindus Drummondii* (Fuhlendorf et al. 2002). Taxonomic nomenclature follows Hatch et al. 1990.

Artificial Nests

Three replicated treatments were established on ca. 45 ha areas that consisted of riparian and upland sites that were subjected to heavy, moderate and ungrazed treatments to determine associations between nest success, grazing, landscape position and vegetation structure. In each of six pastures, we placed 72 artificial nests (432 total nests) along 4 60- x 40-m grids. To determine influence of landscape position on artificial nest success, we placed 2 grids within the riparian and 2 within each upland site. Upland sites were > 100 m from riparian zones because previous studies had indicated that edge effects may occur within 50 m of an edge; Burger et al. 1994). Each grid consisted of 4 nests placed at 20-m intervals along each of 3 transects spaced approximately 20 – 40 m apart, depending on the width of the riparian zone. Riparian zones were divided into 3rds (2 sides and center of drainage), and line transects were established within the center of each 1/3rd. On uplands line transects were generally spaced 20-m apart. At 20-m intervals along each transect we made a small depression and placed 2 quail eggs within each nest site. We did not attempt to reposition or conceal nests because we were interested in determining the influence of grazing and landscape position on vegetation structure and their subsequent influence on artificial nest success. Nest sites were inconspicuously marked with 2-mm diameter metal stakes (standard survey stakes with the flag removed), so that the exact location could be determined at a later date. Nest fate was recorded at the end of 14- and 23-day exposure periods; 23 day exposure is similar to the incubation period local ground-nesting birds. A nest was considered to be depredated if one or both eggs were broken or removed from the site.

Vegetation Structure

To quantify relationships between vegetation structure and artificial nest success we recorded plant vegetation height from the center of each nest site and we determined the angle of obstruction along 8 radii at 45° compass intervals, where mean angles of 90° are completely closed and mean angles of 0° are free from obstruction. This method efficiently quantifies both vertical and horizontal vegetation structure and is an important indicator of ground nesting bird habitat (Kopp et al. 1998, Harrell and Fuhlendorf 2002). We used a 0.25-m^2 quadrat to characterize plant cover. Estimates of percent cover by functional group (grass, forb, shrub, litter and bare ground) were recorded using the mid-point of Daubenmire's cover classes of 0–5, 6–25, 26–50, 51–75, 76–95, and 96–100% (Daubenmire 1959). Because riparian areas were covered by a canopy of trees, vegetation characteristics within the riparian, only included species that were $\leq$ 1.5 m tall.

Statistical Analysis

We compared percent vegetation cover between grazing treatments (heavy, moderate, and ungrazed) and landscape position (riparian, upland) with analysis of variance (SAS Institute Inc. 2001). Sources of variation were distributed among main factor effects (grazing treatment and landscape position). To assess the influence of vegetation coverage variables on nest success, we used stepwise multiple regression analysis (PROC REG; SAS Institute, Inc. 2001), with nest success as the dependent variable and cover of plant functional groups as the independent variables. Variables selected for inclusion in the model were significant when $P \leq 0.15$ (Hosmer and Lemeshow 1989, Sams et al. 1996, Cody and Smith 1997, Bowyer et al. 1999). The suitability of this model was tested using the Hosmer-Lemeshow goodness-of-fit statistic (Hosmer and Lemeshow 1989), where $P > 0.05$ indicated that the model was a suitable fit. We also, examined relationships between cover of plant functional groups and artificial nest success using Pearson correlation analysis (PROC CORR, SAS Institute, Inc. 2001). We determined differences in rates of artificial nest predation using Chi-square analysis (SAS, Institute Inc., 2001).

Results

Of 432 artificial nests, 3 and 21 nest sites could not be relocated after 7- and 23-day exposure, respectively. Total predation on all nests exposed during the entire study period increased from 22% after 7 days to 52% after 23 days of exposure. Vegetation characteristics associated with artificial nest sites were highly variable. Vegetation cover ranged from 0 to 98% and angle of obstruction ranged from 0 to 90°. Heavy grazed sites were associated with greater bare ground than ungrazed sites (Table 1). Shrub cover was slightly higher for nest sites in the moderate grazed treatment. Cover of grass and angle of obstruction were greatest within ungrazed sites (Table 1). Bottomlands were characterized by > 75% tree cover. Cover of plant functional groups and angle of obstruction were generally greatest within the bottomlands (Table 2).

Predator response to artificial nests was dependent on spatial scale. At the local scale (within 0.25-m^2 quadrat), all vegetation cover variables did not differ between successful and depredated artificial nest sites after 7- or 23-days exposure (Table 3). Similarly, we found no difference in angle of obstruction between successful and depredated nest sites after 7-days exposure. The only vegetation characteristic that differed at the smallest spatial scale was angle of obstruction after 23-days exposure. Successful nest sites were associated with greater angles (Table 3), indicating that both vertical and horizontal vegetation structure may be a better indicator of nest success than vegetation cover alone.

At larger spatial scales predator response to artificial nests varied according to grazing treatment and landscape position (Table 4), where nest success was associated positively with vegetation cover and angle of obstruction. Results suggest that in ungrazed bottomlands, where vegetation cover is maximized (Tables 1 & 2), rates of predation are less than expected after both 7- and 23-day exposure periods (Table 4). On uplands, however, differences in vegetation cover associated with grazing treatment, do not influence nest success (Table 4), suggesting that vegetation cover may be an indicator of nest success at larger spatial scales only when vegetation cover and structure is maximized (i.e. ungrazed bottomlands).

Discussion

Livestock grazing often influences wildlife habitat by directly influencing vegetation structure (Dyksterhuis 1949, Ellison 1960, Fuhlendorf and Smeins 1997). Grazing induced changes in vegetation structure and species composition are likely to influence patterns of animal utilization throughout the landscape (Holochek et al. 1989) and may directly alter nest site selection for many grassland species. Our data suggests that livestock grazing has an influence on vegetation cover and structure. Vegetation cover progressively decreased with grazing and was generally greater on bottomlands. Although grazing altered vegetation cover, we found that it had little influence on predicting artificial nest success at the local-scale (within 0.25 m^2 quadrat). Other researchers studying the influence of vegetation on nest success have also documented similar results where nest site selection was unrelated to nest success (LaHaye et al. 1997, Filliater et al. 1994, Yahner and Voytko 1989). Our data suggests successful nest sites were associated with greater angles of obstruction, but these differences were only detectable after the 23-day exposure period. These results suggest that measures of vertical and horizontal structure may be important components when evaluating the influence of nest site selection on rates of predation for many grassland species. These data also suggest that grazing effects on nest predation are complex and nested within the variability caused by landscape patterns.

Various grazing regimes have been responsible for affecting the reproductive success of many grassland species. While some studies show that some species benefit from grazing (Renken and Dinsmore 1987, Knopf 1996), others document negative effects of grazing on nesting success (Weller et al 1958, Koerth et al. 1983). We found that although livestock grazing altered the vegetation patterns (cover and structure) between treatments, it had a limited influence on nest success. Given the similarities of the habitats between heavy and moderately grazed sites (Table 1), it is not surprising that those sites suffered similar rates of predation (Table 4). However, rates of predation were lower than expected on sites that were located within ungrazed bottomlands. Thus, the effects of grazing on nest predation can not be generalized and, on this mixed prairie site, must be considered in the context of variability that occurs within the landscape.

It has been hypothesized that birds select sites with greater concealment presumably because those sites likely increases successful reproduction (Martin 1992, Townsend et al. 2001). Hence, at a larger scale, areas where vegetation cover is maximized (i.e. on sites that are both ungrazed and located within a bottomland) may increase the likely hood of successful reproduction for ground nesting grassland species. There is both supportive and contradictory evidence for this hypothesis. In a study comparing relationships between nest concealment and predation in hooded warbler (*Wilsonia citrina*) nests; nest visibility and vegetation density surrounding the nest did not differ between successful and depredated nests (Howlett and Stutchbury 1996). Further, in the same study, researchers experimentally removed surrounding vegetation to increase visibility. Manipulated nests were 86% more visible than control nests, but they did not suffer higher predation rates. However, other studies have documented the importance of vegetation cover to reducing predation risk (Rands 1986, Martin and Roper 1988, Dion et al. 2000). Similarly, our data is both supportive and contradictory to this hypothesis. For instance, at larger spatial scales, ungrazed bottomlands likely increase chances of successful reproduction, however, the differences between grazed and ungrazed sites on artificial nest success are undetectable on upland sites. Further, at smaller spatial scales, changes in vegetation structure and cover associated with grazing had no influence on nest success.

Livestock grazing is the most prevalent land use on the majority of North American rangelands. Rangelands account for 61% of the land area of the United States (Holechek et al. 1998) and grassland bird species associated with these rangelands are declining at a faster rate than any other guild of birds in North America (Knopf 1994). Thus, understanding relationships between grazing and grassland birds has the potential to dramatically influence populations of this imperiled guild throughout the Great Plains of North America. As a result, our objective was to determine whether ground nest predation was related to specific site characteristics influenced by grazing. Our data suggests that grazing has a minimal influence on rates of predation. However, this conclusion does not suggest that grazing has no effect on grassland birds. Habitat alterations associated with grazing on grasslands could be related to other factors of avian ecology, such as food availability and foraging opportunities, influencing energetic costs, or regulating operative temperatures.

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Table 1. A comparison of vegetation characteristics (percent ground cover, and angle of obstruction) between grazing treatments on Marvin Klemme Range Research Station, Bessie, Oklahoma, 2000.

	Heavy[a,b]		Moderate[c]		Ungrazed	
	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*
Bare ground	$27^{ns,**}$	2.69	21^{ns}	2.50	16	2.19
Leaf litter	$7^{ns,ns}$	1.69	10^{ns}	2.02	8	1.77
Grass	$46^{ns,**}$	2.81	46^{**}	3.08	58	3.12
Forb	$20^{ns,ns}$	1.60	16^{ns}	1.41	17	1.65
Shrub	$10^{***,ns}$	1.67	21^{***}	2.63	10	1.93
Angle of obstruction (°)	$64^{ns,***}$	1.80	69^{***}	1.66	76	1.64

Significance indicated by: ^{ns} = nonsignificant, $^{*}P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$, $n = 144$.

[a] ANOVA test for heavy vs. moderate treatments.

[b] ANOVA test for heavy vs. ungrazed treatments.

[c] ANOVA test for moderate vs. ungrazed treatments.

Table 2. A comparison of vegetation characteristics (percent ground cover, and angle of obstruction) between landscape positions (bottomland, upland) on Marvin Klemme Range Research Station, Bessie, Oklahoma, 2000. $n = 216$.

Vegetation characteristic	Bottomland		Upland			
	$\bar{x}$	*SE*	$\bar{x}$	*SE*	*F*	*P*
Bare ground	19	2.15	24	1.90	2.16	0.143
Leaf litter	14	1.99	2	0.40	37.26	<0.001
Grass	47	2.60	54	2.34	3.43	0.065
Forb	20	1.54	16	0.93	5.18	0.023
Shrub	17	2.12	11	1.27	7.19	0.008
Angle of obstruction (°)	72	1.54	68	1.29	5.54	0.019

Table 3. Comparison of percent ground cover and mean angle of vulnerability for successful and depredated artificial nest sites in Washita County, Oklahoma, June 2000.

Artificial Nest Exposure	Successful			Depredated				
Coverage and Angle	*n*	$\bar{X}$	*SE*	*n*	$\bar{X}$	*SE*	*F*	*P*
7-days								
Bare ground	333	21.4	1.59	96	22.9	3.33	0.19	0.665
Leaf litter	333	7.4	1.13	96	11.3	2.67	2.32	0.129
Grass	333	49.9	1.97	96	50.3	3.85	0.01	0.930
Forb	333	18.2	1.05	96	16.48	1.77	0.64	0.424
Woody	333	13.7	1.36	96	14.32	3.03	0.04	0.840
Angle	333	70.2	1.09	96	67.7	2.47	1.06	0.304
23-days								
Bare ground	188	18.4	1.90	223	23.5	2.11	3.14	0.077
Leaf litter	188	6.3	1.34	223	9.4	1.58	2.16	0.142
Grass	188	53.9	2.66	223	48.6	2.40	2.15	0.144
Forb	188	19.2	1.49	223	16.6	1.10	2.04	0.154
Woody	188	12.6	1.67	223	12.9	1.71	0.02	0.879
Angle	188	72.2	1.43	223	67.4	1.47	5.45	0.020

Table 4. Comparison of depredated nests between grazing treatments within bottomland and upland sites in Washita County, Oklahoma, June 2000.

	Nests depredated											
	Heavy			Moderate			Ungrazed					
Exposure Treatment	*n*	E^*	%	*n*	E^*	%	*n*	E^*	%	*df*	χ^2	*P*
7-day												
Bottomland	16	17	31	24	17	46	12	17	23	2	5.95	0.051
Upland	20	15	45	11	15	25	13	14	30	2	3.70	0.158
23-day												
Bottomland	47	38	42	41	37	37	24	37	21	2	16.38	<0.001
Upland	39	36	35	39	37	35	33	37	30	2	1.62	0.445

E^* = Expected Chi-Square Frequencies.

#7

VITA

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Candidate for the Degree of

Doctor of Philosophy

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