SMALL MAMMALS IN DISTURBED TALLGRASS PRAIRIE LANDSCAPES

by

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B.S., Kansas State University, 2007

A THESIS

Submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2012

Approved by:

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Abstract

Disturbance is defined as any discrete event that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment. Habitat use by an organism is based on its perception of where to maximize its own fitness, and can be altered in response to disturbance-induced changes in resources, substrate, or physical features modified by disturbance. Disturbance-induced changes to vegetation structure reshape a small mammal's surrounding physical environment and/or resources, and may influence its utilization of an area. Effective wildlife and resource management is dependent on a thorough understanding of how individual species and communities utilize their surroundings and how disturbance affects a species' response to changes in its surroundings.

We investigated seasonal habitat associations of three small mammal species and for overall species diversity across a gradient of military combat-vehicle disturbance intensities at the Fort Riley Military Reservation, Kansas. Deer mouse (*Peromyscus maniculatus*) abundance did not vary across a categorical gradient of disturbance created by military-combat vehicles, regardless of season. Western harvest mouse (*Reithrodontomys megalotis*) abundance was associated with more highly disturbed areas irrespective of season. Prairie vole (*Microtus ochrogaster*) abundance was associated with habitat that was less disturbed in the spring but more highly disturbed in the fall. Shannon diversity of the small mammal community was higher in the more highly disturbed areas regardless of season. This research shows that small mammals respond to disturbances created by military training with combat vehicles in a species-specific manner, and indicates that there may be differences in the effects of military training versus natural or agricultural disturbances on the abundance and diversity of small mammals. This is an important consideration given that the Department of Defense manages more than 12 million ha of land in

the United States, and is charged under the Sikes Act with conserving natural resources on these lands, including biological diversity. Thus, the findings of other ecological research on the effects of disturbance on small mammals may not be directly applicable to the types of disturbances that occur on military lands, which underscores the need for further research on the specific effects of military-training activities on species' responses.

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Introduction

Small mammals are important components of tallgrass prairie ecosystems, functioning as both predators and prey. Individual species of small mammals prey upon insects and other small invertebrates, while other small mammals eat seeds and/or vegetation. Small mammals, in turn, are an important food source for a range of grassland predators including the Red-tailed Hawk (*Buteo jamaicensis*), Great Horned Owl (*Bubo virginianus*), Red Fox (*Vulpes vulpes*), Coyote (*Canis latrans*), and the American Badger (*Taxidea taxus*). Many small mammal species inhabit tallgrass prairies, and their habitat associations can range from generalists to specialists. The health of a tallgrass prairie as it relates to wildlife habitat, as well as the ecological health (Pitts et al. 1987) of that area, can be assessed by measuring changes in small mammal attributes such as diversity or abundance, because of their sensitivity and predictable responses to habitat changes (Olsen and Brewer 2003).

Disturbance was once defined as any partial or total removal of biomass (Grime 1979). White and Pickett (1985) expanded this definition to "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." Impacts from disturbance on an ecological system can vary, and are dependent on a number of features including: distribution in space, frequency of occurrence, predictability of occurrence, area covered, and intensity (Rykiel 1985, Turner 1989, White and Pickett 1985).

Disturbance regimes are important components of ecological systems, and may control succession and community function (Collins et al. 1998). Causes of natural disturbance may be abiotic factors such as fire, floods, drought, and wind; or biotic factors such as predation or grazing (Sousa 1984). Depending on its spatial distribution, disturbance has the potential to limit the distribution of native species (Bestelmeyer et al. 2003) which may allow for the influx of non-native species (Masters and Sheley 2001).

Perception and utilization of an area by an organism are dependent on natural-history traits such as its size and mobility (Vos et al. 2001). A species' distribution across a landscape depends on how individuals of that species select particular habitat characteristics (Rowe 2007). Individuals are expected to select habitat in a way that maximizes their own fitness (Morris 1987; Wiens 1976). Fitness may depend on a number of factors such as the availability of food, shelter, and mates, competition, or risk of predation (Rosenzweig 1981). Modification of a landscape due to succession or disturbance can also affect an organism's perception of that habitat (Morris 1990), thereby altering its habitat use (Rowe 2007).

Military combat-vehicle training is a form of anthropogenic disturbance that directly impacts soil and vegetation communities (Diersing et al. 1988; Leis et al. 2005; Van Horne and Sharpe 1998), with both direct and indirect effects on vertebrate communities (Leis et al. 2007; Li et al. 2006). Training with military combat vehicles, such as the M1A2 tank (57,000 kg), can create substantial disturbance including removal of vegetation, soil compaction (Johnson 1982; Li et al. 2006 ; Milchunas et al. 2000; Prosser et al. 2000; York et al. 1997), and the creation of large areas of bare ground (Althoff et al. 2006). Combat-vehicle training may directly influence small mammals through soil compaction and crushing small mammal burrows, and indirectly through removal of biomass used for cover and foraging. The effects of military disturbance have important conservation consequences. The Department of Defense manages more than 12.1 million hectares of land (Stein et al. 2008), and military disturbances are likely distinctly different from natural disturbances (Quist et al. 2003).

The goal of this study was to investigate seasonal habitat associations of small mammals in tallgrass prairie ecosystems, specifically in relation to a gradient of disturbance caused by military combat-vehicle training at the Fort Riley Military Installation, located in the Flint Hills region of northeast Kansas. Previous research on lightly and heavily disturbed areas of Fort Riley found species richness of small mammals to be lower on heavily disturbed areas (Conard 2003). We expanded on this study and looked at a gradient of disturbance to examine how small-mammal habitat associations changed with increasing disturbance from military training with combat vehicles. We sought to address two questions in this study. First, do small mammal habitat associations change in relation to a gradient of disturbance from military training with combat vehicles? Second, does the species composition of the small mammal community change in response to the aforementioned disturbance? We tested specific hypotheses as to how species should respond to disturbance intensity, based previous research on the habitat associations of these small mammals (Figure 1), and hypothesized that species diversity (H') would be highest at some intermediate level of military training disturbance (i.e., intermediate disturbance hypothesis; Connell 1978).

Methods

Fort Riley is a 40,273-ha military training facility located in Clay, Geary, and Riley counties in the Flint Hills of northeastern Kansas (39°15'N, 96°50'W). The Flint Hills region encompasses over 1.6 million ha (Figure 2) covering a large portion of eastern Kansas. This area contains the largest remaining areas of unplowed tallgrass prairie in North America (Reichman 1987). The area of tallgrass prairie on Fort Riley are larger than the areas of remaining tallgrass prairie found in Illinois, Indiana, Iowa, North Dakota, and Wisconsin combined (Samson and Knopf 1994).

There are three dominant land-cover types on Fort Riley: grasslands (ca. 32,200 hectare), woodlands (ca. 6000 hectare), and shrublands (ca. 1600 hectare). Dominant grassland species include big bluestem (*Andropogon gerardii*), Indiangrass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium*), and switchgrass (*Panicum virgatum*), with other grass and forb species occurring at lower abundances. Dominant woodland species include chinquapin oak (*Quercus muhlenbergii*), bur oak (*Quercus macrocarpa*), American elm (*Ulmus americana*), hackberry (*Celtis occidentalis*), and black walnut (*Juglans nigra*). Shrublands are dominated by rough-leaved dogwood (*Cornus drummondii*), smooth sumac (*Rhus glabra*), and buckbrush (*Symphoricarpos orbiculatus*), occurring with interspersed grasses and forbs (Althoff et al. 2006).

The topography at Fort Riley consists of rolling hills of upland prairie with gallery forests in ravines and lowland areas. There are 36 soil series on Fort Riley grouped into six soil associations. The Wymore-Irwin, Clime-Sogn, Benfield-Florence, and Smolan-Geary are the most abundant associations making up roughly 85% of Fort Riley (USDA Soil Conservation Service 1996), with the Wymore-Irwin being the most common in the grasslands (Althoff and Thien 2005). All of our study sites fell into the Wymore-Irwin association.

Military training at Fort Riley causes a variety of disturbances from activities such as field maneuvers, combat-vehicle training, troop encampments, and artillery fire. Wildfires may occur due to training activities during any season. Vegetation management consists of mowing, chemical control of noxious weeds, prescribed burning, and small-scale timber harvest (U.S. Army 1994). The focus of our study was on the effects of combat-vehicle training.

To identify potential study sites, a list of 500 possible study plot locations across the Fort Riley landscape was generated using the Generalized Randomized Tessellation Stratified

(GRTS) design (Theobald et al. 2007). The GIS program ArcGIS (ESRI, Redlands California) was used to apply this stratification design using the Reversed Randomized Quadrant-Recursive (RRQR) tool (Theobald and Norman 2006). This type of probability-based design randomly selects spatially balanced sampling locations across a landscape, which allows for sound statistical inference (Theobald et al. 2007) and provides for the addition or removal of sites without loss of statistical power. Because this implementation of GRTS operates in an ArcGIS environment, it can utilize both complex domains and complex variable sampling rates specified as a GIS probability surface. For example, we were able to restrict all plot edges to be at least 50 meters from established roads. Other constraints on plot selection are listed in Table 1.

Thirty-two plots selected from the GRTS-generated list were used as sampling locations in this study. Each plot was 100 m by 100 m (i.e., 1 ha). Plot selection was based on an estimated level of military combat-vehicle training disturbance in an effort to include equivalent numbers of samples representing the full range of disturbance intensities. These disturbances included: crushing of vegetation where vehicles drove through an area, removal and piling of vegetation and dirt where tanks and/or other track-type vehicles had performed tight turns, and areas where repeated passes of vehicles left only soil. Disturbance estimates were obtained by visiting the GRTS list locations and visually estimating the level of disturbance. Sites were categorized into one of four disturbance categories: 1) no disturbance, 2) low disturbance, 3) medium disturbance, and, 4) high disturbance. Disturbance categories were used to ensure that a gradient of disturbance was being sampled during each trapping session, with one plot from each disturbance category sampled each week (n = 8 plots/disturbance category).

One hundred small-mammal trap stations were located on each plot in a 10 by 10 grid pattern of large non-folding Sherman live traps (7.6 x 8.9 x 22.9 cm). Each 100 m by 100 m (1 ha) plot had a distance of 9.1 m between trap stations and a 9.1 m buffer to the edge of the plot. Locations of each trap station were marked with a Trimble GeoXT, using differential corrections so that the same locations could be re-trapped in the fall (see below). Spring sampling of small mammals took place over eight weeks during March and April 2008; fall sampling through October and November. Each week, four sites were simultaneously sampled over four consecutive nights, with one site being selected from each of the preliminary disturbance categories. The same sites were sampled in both spring and fall.

A single trap was set at each station and baited with black oil sunflower seeds. A ball of polyester fiberfill was added for bedding. Captures were identified to species, gender, age class, reproductive status, and mass to the nearest half gram. Newly captured individuals were uniquely marked, either with an ear tag (National Band and Tag # 1 monel), or by trimming a unique mark into the fur of the abdomen (for shrew or young vole species). After processing, each small mammal was released at the site of its capture.

Tests of small mammal habitat associations were conducted using a nested ANOVA design, with season as a repeated measure. The count of unique individuals for each species of small mammal was used as the response variable. A Tukey (HSD) test was used to test for significant differences between disturbance categories. To test for significant differences in species composition in relation to disturbance at Fort Riley, Shannon-Wiener diversity ($H' = -\Sigma (p_i \ln[p_i])$) indexes were calculated for each 1.0-ha plot. The relationships between disturbance category and diversity were then analyzed using a one way ANOVA and a Tukey HSD test.

Results

With 13,200 trap-nights, we captured 2068 small mammals of 12 species during both the spring (415 individuals) and fall (1653 individuals) trapping seasons (Table 2). Three species, deer mice (*Peromyscus maniculatus*), western harvest mice (*Reithrodontomys megalotis*), and prairie voles (*Microtus ochrogaster*), were the only species captured during both the spring and the fall and on all 32 study plots. These three species accounted for 81% of the total number of individuals captured. We therefore limited our analyses of habitat associations to these three species.

Disturbance intensity did not have a significant effect on the abundance of deer mice in either season, which were uniformly abundant across the study area ($mean$ = 18, sd = 30). In contrast, the abundance of western harvest mice varied among disturbance categories ($F_{1,14}$ = 5.77, $P = 0.002$), although abundance was significantly higher in sites that had either a low or high level of military-training disturbance than undisturbed sites (Figure 3). Prairie voles showed differential association among disturbance categories ($F_{1,14} = 15.51$, $P = 0.001$) and seasons ($F_{3,28} = -2.89$, $P = 0.04$; Figure 4).

Small-mammal diversity (H') differed among disturbance categories in the spring ($F_{3,38}$ = 10.17, $P < 0.0001$), and was highest within sites that experienced an intermediate to high level of military-training disturbance (Figure 5). In the fall, small mammal diversity followed a similar pattern with diversity highest in highly disturbed sites ($F_{3,38} = 4.31$, $P = 0.01$; Figure 5).

Discussion

Grasslands experience a range of natural or agriculturally induced disturbances, including livestock grazing and trampling (Hobbs and Huenneke 1992), fire (Hulbert 1986), soil erosion (Pimentel and Kounang 1998), and soil compaction (Ball et al. 1997; Hamza and Anderson 2005). These sorts of disturbances can alter vegetation structure in a manner that decreases habitat suitability for native species (Hobbs and Huenneke 1992; Soule 1990; Westman 1990). These disturbance-induced changes in habitat suitability may alter an organism's perception of that habitat (Morris 1990), thereby altering its use of the habitat. Disturbance from military training with combat vehicles has been documented to increase areas of bare ground, compact the soil, and increase soil erosion (Althoff et al. 2006; Johnson 1982; Li et al. 2006; Milchunas et al. 2000; Prosser et al. 2000; York et al. 1997). These disturbance-induced changes to the Fort Riley landscape create a mosaic of habitat from which small mammal species select habitat to use based on their resource needs.

Deer mice are often considered habitat generalists and are known to utilize a wide range of habitat types (Wywialowski 1987). This species has long been known to prefer open or early-seral habitat (Smith 1940; Wecker 1963), and occur at reduced abundances in dense (Lobue and Darnell 1959) or tall (Wetzel 1958) vegetation. Using these known habitat associations, we hypothesized this species would be most associated with areas having increased disturbance levels. However, deer mice in this study did not indicate significant associations to any of our disturbance categories related to military combat-vehicle training. Deer mice followed their habitat generalist nature and were present in equal abundances on plots at Fort Riley regardless of the amount of disturbance from military training with combat vehicles.

Western harvest mice utilize a wide range of habitat types, but are usually associated with grassy or weedy areas, and abundances have frequently been documented as higher in areas with tall, dense vegetation than in areas without (Webster and Jones 1982). We hypothesized that western harvest mice would be associated with areas receiving intermediate disturbance levels where they would have tall, dense vegetation present and possibly reduced numbers of competitors such as prairie voles and cotton rats (*Sigmodon hispidus*) (Johnson and Gaines 1988). This species did not follow our predicted pattern of habitat association, with the highest degrees of association on highly and intermediately disturbed plots (Figure 3) and we do not have an explanation for this pattern of habitat association. However, it is possible the military combat-vehicle training disturbance during spring created runways that persisted into the fall, which increased captures of this species on highly disturbed study plots (Pearson 1960).

Prairie voles prefer habitat with dense vegetation (Kaufman and Kaufman 1989) in which it creates runway systems (Kaufman and Fleharty 1974) to access food sources. In the Kansas summer months, the main food source for voles is plant material (Fleharty and Olsen 1969). Following these known habitat associations, we hypothesized that prairie voles would be most associated with lower levels of disturbance by military vehicle training, resulting in less vegetation removal. In the spring, prairie voles were captured more frequently in areas that had lower levels of disturbance, but in the fall, this species was most associated with higher disturbance categories (Figure 4). The association of prairie voles with more highly disturbed habitat in the fall may seem counterintuitive; however, the primary cause of disturbance in this study was military training with combat-vehicles (i.e., humvees, tanks and armored personnel carriers). Spring sampling in this study took place during a period of heavy military training, prior to the Department of Defense shipping heavy mechanized vehicles from Fort Riley to the war in Iraq. Subsequently, relatively little military training with combat vehicles occurred on our study plots during the summer and fall. Areas that were highly disturbed in the spring season typically had fresh vegetative re-growth in the fall. This fresh growth in the fall likely drove this habitat association.

Small mammal diversity increased with increasing disturbance by military combat vehicles on the Fort Riley Military installation. This is counter to our expectation that diversity estimates would be highest at and intermediate level of disturbance. There are numerous possible explanations for this observed diversity pattern. The most likely is the fact this study was conducted during two seasons of one year, which may not have allowed for decreases in rare or habitat specialist species to disappear from the landscape over the course of this study (Andren 1994).

In summary, deer mice did not indicate significant habitat associations to any of our disturbance categories. Western harvest mice were associated with disturbance categories two and four, with no significant associations between seasons. Prairie voles showed variation in habitat association among disturbance categories and seasons. Shannon diversity increased with increasing disturbance, with the highest diversity found in the most heavily disturbed areas in both the spring and fall.

Small mammals are not the only group of animals that have been shown to alter their habitat use due to natural or anthropogenic disturbances, and that would likely alter their use of habitat due to military training with combat vehicles. For example, many native North American grassland bird species select habitat for nesting based on vegetation density and structure and are either negatively or positively affected by haying (Perlut et al. 2006), fire (Cully and Michaels 2000; Walk and Warner 2000), and grazing and prescribed burning (Walk and Warner 2000; Rahmig et al. 2009). Invertebrate species such as beetles (Louzada et al. 2010), butterflies (Poyry et al. 2004), and grasshoppers (Joern 2005) also are affected by the same types of disturbances.

Among Federal agencies, the Department of Defense manages one of the largest areas of land in the United States and harbors 23% of the endangered and 15% of the imperiled species (Stein et al. 2008) in the country. Given the large land area managed by the military, the impact that military training has on soil and vegetation communities, and the correlations between disturbance due to military training and other types of disturbances, the potential impacts of military training on threatened and endangered wildlife and plants are significant. Our research indicates that the effect of military training with combat vehicles on Fort Riley creates a disturbance mosaic that differentially influences the abundance and distribution of small mammals. In this study, two of the three species of small mammals did not respond as hypothesized, based on previous ecological research on small-mammal responses to grassland disturbance (e.g., grazing and prescribed burning). This underscores the importance of further research into military-training effects on other species and on other military installations is truly warranted, as it may not be possible to extrapolate from other ecological research to predict the consequences of military disturbances on species responses..

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Figures and Tables

Table 1 Criteria for elimination of plots at Fort Riley, using GRTS design in ArcGIS to select potential plot locations.

1) In a riparian/wooded area
2) Within 50 meters of maintained road
3) Falls in an area not accessible by non-military personnel (i.e. impact zone)
4) Intersected by intermittent or perennial stream
5) Intersected by pond
6) Contains a chain-link fence
7) Inside wildlife food plot or recently restored grassland
8) Contains quarry, borrow pit, or other excavated area
9) Scheduled for a controlled burn during trapping season

Table 2 Number of unique individuals, and total number of captures (in parenthesis) from 12 species of small mammal captured on 32 study plots across the Fort Riley Military Reservation during the spring and fall of 2008.

Species	Spring	Fall
Blarina hylophaga	1(1)	74(207)
Chaetodipus hispidus	2(6)	8(10)
Cryptotis parva	0	3(3)
Microtus ochrogaster	63(163)	479(692)
Mus musculus	0	2(2)
Neotoma floridana	5(8)	2(7)
Peromyscus leucopus	25(74)	43(95)
Peromyscus maniculatus	107(449)	315(728)
Reithrodontomys megalotis	197(733)	565(903)
Reithrodontomys montanus	9(15)	13(17)
Sigmodon hispidus	6(17)	147(248)
Zapus hudsonius	0	2(2)

Table 3. Summary of a repeated measures analysis of variance on the effects of season (spring vs. fall) and disturbance intensity (four categories) created by military combat vehicles on the abundance of three small mammal species at the Fort Riley Military Installation, Kansas in 2008.

Species	Effect	F	DF	P
Deer Mouse				
	Season	3.04	1,14	0.1
	Disturbance Category	1.85	3,42	0.15
	Interaction	0.74	3,42	0.54
Western Harvest Mouse				
	Season	0.88	1,14	0.36
	Disturbance Category	5.77	3,42	<0.001
	Interaction	0.46	3,42	0.71
Prairie Vole				
	Season	15.51	1,14	0.001
	Disturbance Category	2.89	3,42	0.04
	Interaction	3.55	3,42	0.02

Figure 1 Diagram depicting the hypothesis between species abundance and disturbance intensity for three small mammal species on the Fort Riley Military Installation, Kansas.

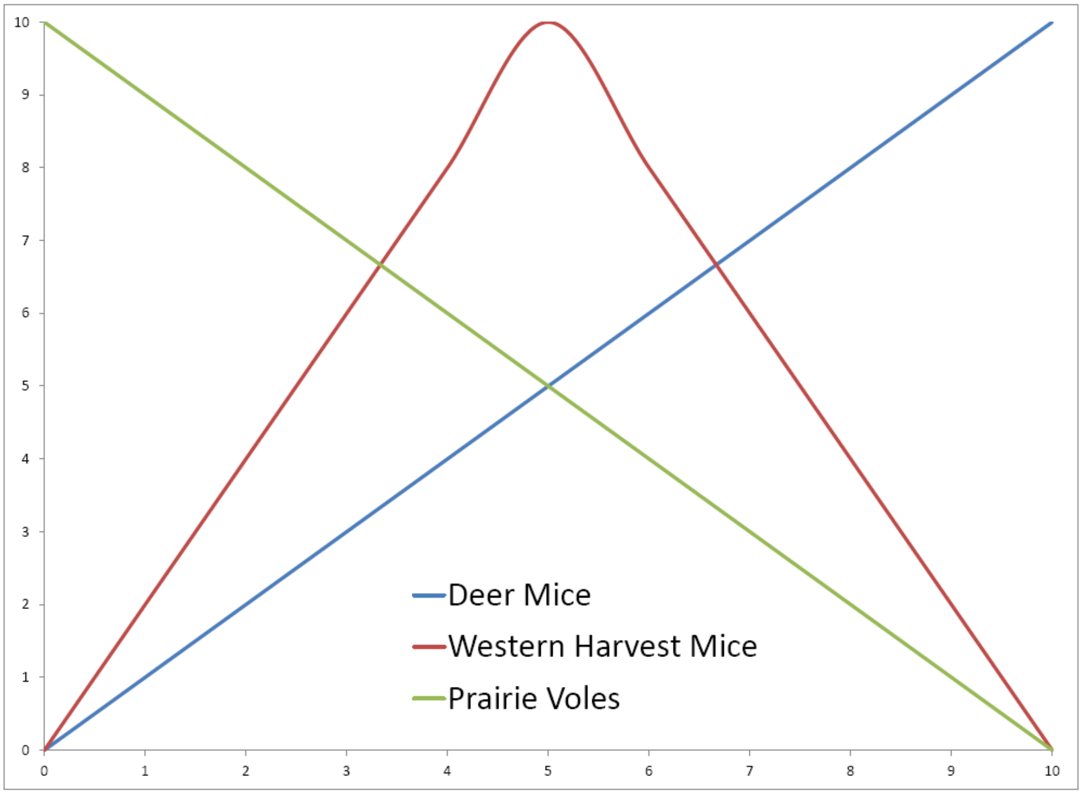

Figure 2 The Fort Riley Military Reservation (right) is located in the Flint Hills (center) of Kansas. Field sites for this study were dispersed across the Fort Riley landscape, with the exception of the impact area (red area) which is closed to non-military personnel.

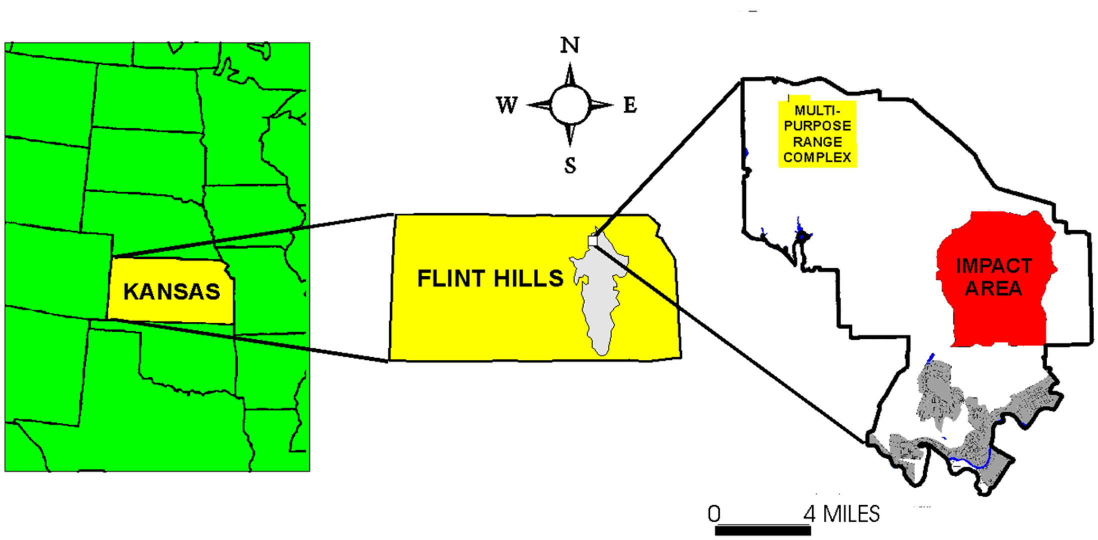

Figure 3 Western harvest mouse habitat associations from 32 study sites across four disturbance categories on the Fort Riley military installation in the spring and fall of 2008. Variation between disturbance categories was significant (Table 3).

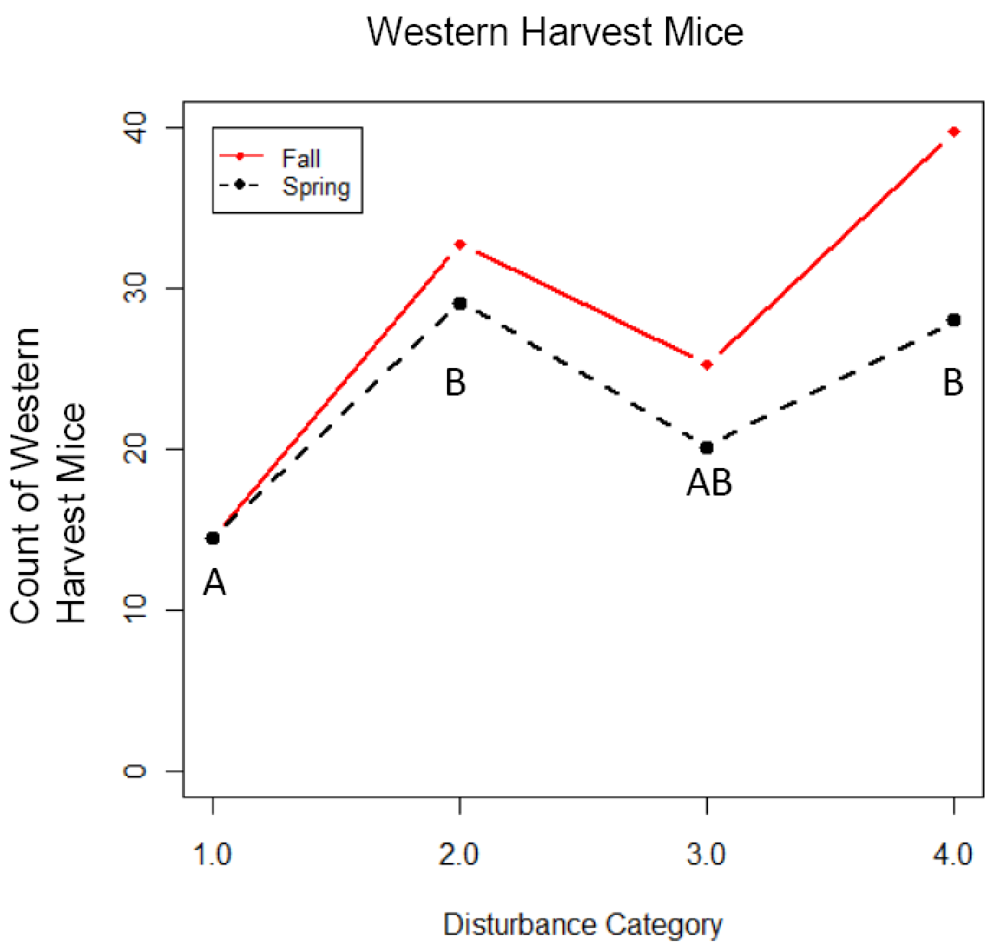

Figure 4 Prairie vole habitat associations from 32 study sites across four disturbance categories on the Fort Riley military installation in the spring and fall of 2008. Variation in season and category were significant (Table 3). Variation between seasons was significant.

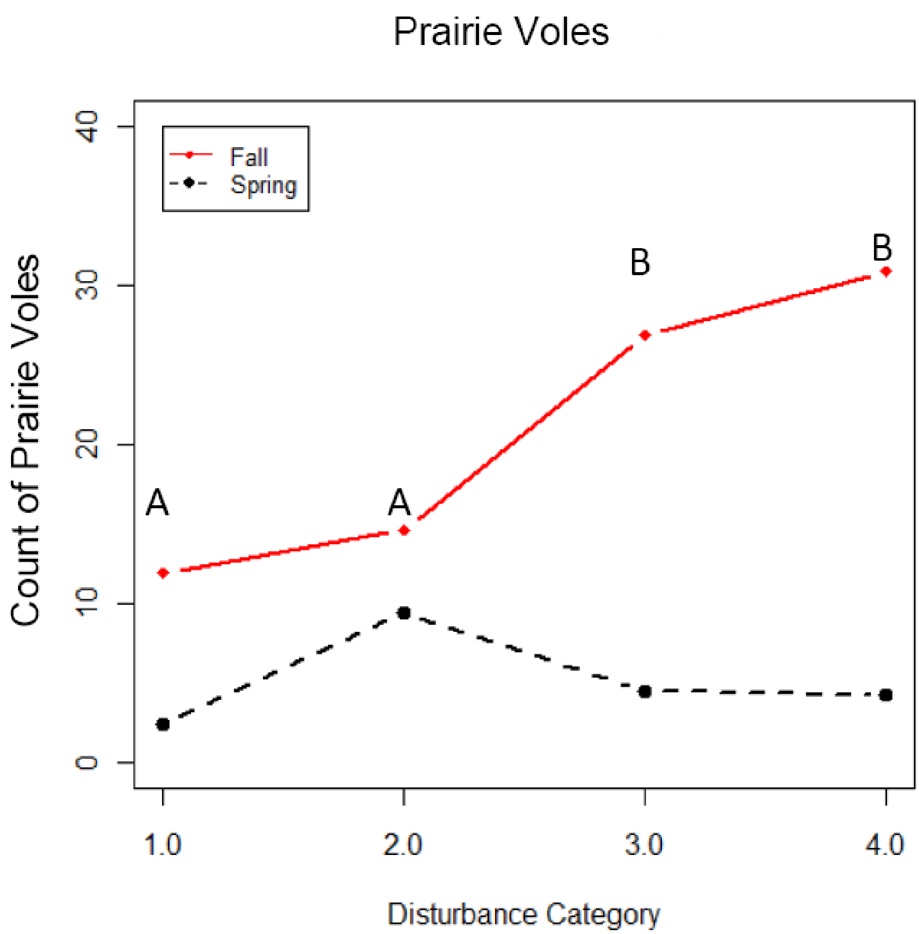

Figure 5 Shannon diversity (H') across four disturbance categories on the Fort Riley Military Installation, Kansas in the spring and fall of 2008.