SMALL RODENT DIVERSITY AND HABITAT UTILIZATION OF HEAVILY GRAZED SHORTGRASS RANGELAND OF THE EDWARDS PLATEAU

THESIS

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By

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DEDICATION

To my sons,

Danny and Marc

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CHAPTER 1

INTRODUCTION

Changes induced by ungulate grazing on the local environment have been documented across a wide range of North American grassland types (Grant et al., 1982). Grazing alters the structure of native biotic communities, affecting changes in plant species composition and diversity, primary productivity, and standing crop biomass. Abiotic components of grassland ecosystems, such as soil characteristics, erosion potential, and sediment build-up in waterways, are impacted as well (Grant et al., 1982). Differences in plant species composition and vegetative structure are apparent on grazed versus ungrazed sites on grasslands of the Southwest (Smeins and Merrill, 1988; Holechek et al., 1994; Bich et al., 1995; Scholl and Kinucan, 1996; Bock and Bock, 1997). Heavy grazing of grasslands of the Edwards Plateau, for example, inhibits succession from a shortgrass to a midgrass rangeland (Smeins and Merrill, 1988). Holechek et al. (1994) determined that intermediate grazing of Chihuahuan desert rangeland caused an increase of noxious plant species, while conservative grazing allowed perennial grass cover to increase to twice the amount of standing crop at season's end compared to intermediately grazed sites.

In addition to assessing effects on native floras, several studies have quantified the effects of grazing on wildlife populations and community structure of native faunas (Grant et al., 1982; Bich et al., 1995; Brooks, 1995; Rosenstock, 1996). Effects on wildlife communities can include changes in species composition, diversity, and abundance. The impact of grazing on small rodent populations in particular may be significant because of their functional role in grassland ecosystems (Carey and Johnson, 1995). Rodents are a prey source for reptiles, raptors, and other mammals, but are also predators. Some species are herbivorous, consuming herbage, seeds and berries, while others are omnivorous and include insects in their diets. Thus, monitoring small rodent communities may provide insights into the effects of grazing on higher trophic levels and biodiversity in general (Rosenstock, 1996).

Small mammal faunas are less affected by changes in plant species composition resulting from grazing than by alterations in the physiognomy of the plant community (Grant et al., 1982). Vegetative structure (i.e., the horizontal and vertical distribution of plants within a habitat) provides a variety of cover opportunities for small mammals. In a study of North American grasslands, Grant and Birney (1979) demonstrated that aboveground plant biomass, or cover, had a direct influence on the characteristics of small mammal grassland communities. Available cover influences total biomass of small mammals, species diversity, and specific taxa represented. Functional roles within the community, for example, reproductive strategies, diet, seasonality of activity, are also influenced by the amount of available cover. Because grazing reduces the density of aboveground plant biomass, small mammal faunas are necessarily affected. However, not all grassland faunas are impacted equally or in the same way, i.e., reductions in cover do not yield predictable patterns across grassland types (Grant et al., 1982).

When grazed and ungrazed sites were compared within the same grassland type, significant differences in total biomass of small mammals, faunal diversity, evenness, and proportional species and functional group compositions were evident at tallgrass and montane grassland sites (Grant et al., 1982). Small mammal communities of shortgrass and bunchgrass sites, however, were not significantly affected by different grazing treatments. Species adapted to shortgrasses or sparse cover conditions were less impacted by reduced cover caused by grazing. This differential response was explained by Grant et al. (1982) as due to the greater impact grazing had on cover at tallgrass and montane sites. The greater the changes in available cover, the greater the impact on native small mammal faunas. One can conclude that cover plays a large role in determining small mammal community characteristics in grassland ecosystems.

More contemporary studies have elucidated significant changes induced by grazing on small mammal faunas of arid, desert grasslands. Brooks (1995) found that rodent density and diversity of grasslands of the Western Mojave Desert were significantly higher in areas protected from grazing. A significant increase in seed bank biomass, resulting from increased aboveground plant biomass, was also evident in exclosure areas. Rosenstock (1996) reported that herbaceous vegetation recovered significantly on sites with curtailed grazing relative to sites continuously grazed on semi-arid grasslands in south central Utah. Rodent species richness and abundance were also significantly higher at the macrohabitat level.

Bich et al. (1995) found that intensive grazing altered the richness of the grassland community in the Glen Canyon region of Utah. Heavily grazed pastures exhibited a significant decrease in plant densities. The basal area of some plant species decreased as well. Although total rodent abundance was not significantly different between sites with different grazing intensities, two rodent species in particular, *Perognathus longimembris* and *Peromyscus maniculatus,* responded differentially to grazing. *Perognathus longimembris,* a species of particular importance in the seed dispersal of *Oryzopsis hymenoides,* declined significantly in abundance on heavily grazed sites, negatively impacting rangeland recovery.

Few studies of grassland faunas have assessed the influence of grazing on small mammals in associated riparian habitats. Riparian areas are characterized by high vegetative heterogeneity and support a higher diversity of wildlife than adjacent uplands (Schulz and Leininger, 1991). Riparian grazing can cause extensive damage to the plant community through overgrazing, trampling of vegetation, and compaction of soils. Increased erosion of soils along stream banks and the build-up of sediment in waterways can also result from riparian grazing (Baccus, in press). Schulz and Leininger (1991) demonstrated that although small mammal diversity did not differ between grazed and ungrazed riparian habitats, there was little similarity in the species composition of small mammal communities. *Zapus princeps* was the most abundant small mammal in ungrazed riparian areas, but was not well represented in grazed riparian sites, which lacked sufficient cover. Species adapted to sparse cover conditions, such as *Peromyscus maniculatus,* were abundant in the grazed riparian areas and rare in exclosure sites. Thus, if riparian and adjacent upland sites are assessed together at the landscape level, there is a net decrease in diversity where grazing occuurs.

Intensive grazing may well have deleterious effects on wildlife communities; however, some studies provide evidence that conservative, well-managed grazing may benefit wildlife diversity (Hall and Willig, 1994; Smith et al., 1996; Baccus, in press). Grazing can be used as an effective management tool in maintaining and even restoring grasslands (Smeins and Merrill, 1988; Holechek et al., 1994). Since the Oligocene, North American grasslands have been shaped by a myriad of ecological processes. Grazing by ungulates represents but one of a number of natural disturbances in grassland ecosystems that influenced an ever-changing assemblage of plants and animals over time (Baccus, in press). Wildlife diversity may be maximized by intermediate levels of disturbance that allow for maintenance of mid-successional seral stages. For example, Smith et al. (1996) found that on good condition rangeland (72% of climax vegetation remaining), wildlife diversity was higher than on rangeland in excellent condition (86% of climax vegetation remaining). They ascribed this difference to the higher mix of grasses, forbes, and shrubs on grasslands in good condition; this heterogeneity provided a greater variety of food and cover opportunities for wildlife. In short, whether a site is grazed or not is less critical to wildlife diversity than the kind of disturbance, whereby intensity, duration, and frequency of disturbance are decisive factors (Baccus, in press).

Structural attributes of the environment largely determine habitat selection by small mammals, resulting in a non-random, patchy distribution of species across a heterogeneous landscape (Baccus and Horton, 1984). Habitat selection (and conversely, habitat avoidance) is defined as use of habitat resources disproportional to habitat availability (Litvaitis et al., 1996). In order to support the hypothesis of habitat selection, one must *demonstrate significant and interpretable differences between rodent microhabitats* (M'Closkey and Fieldwick, 1975). Research on habitat selection among small mammals has proliferated in the last two decades. The standard approach has been to test for differential use of quantitatively defined microhabitats (Kaufman and Kaufman, 1989). Many studies have focused on the genus *Peromyscus*, especially *P.*

leucopus and *P. maniculatus*. Habitat features have been identified (at macrohabitat and microhabitat levels) that correlate significantly with species presence (Rosenzweig and Winakur, 1969; Holbrook, 1978; Kantak, 1996; Songer et al., 1997). Selection for certain structural features of the environment can also explain niche separation of sympatric rodents (M'Closkey and Fieldwick, 1975; Stahl, 1980; Parren and Capen, 1985).

The actual features that elicit a response in the selection of habitat often remain unclarified due to the complexity of the environment (Kantak, 1996). For example, the white-ankled mouse, *Peromyscus pectoralis,* is associated with rocky substrates throughout its distribution (King, 1968), suggesting selection for this habitat feature. However, it may be responding to untested covariates. Certainly, other factors also influence the realized niche of a species, including physiology, genetic predisposition, interspecific competition, and predation (M'Closkey and Fieldwick, 1975; Holbrook, 1978; Baccus and Horton, 1984).

The study site investigated in this research was located in the Edwards Plateau Ecological Region and afforded an opportunity to study small rodent populations in a setting that characterizes much of the Texas Hill Country and the Edwards Plateau. The site was a severely grazed shortgrass rangeland with low available cover. The purposes of this study were: 1) to measure the diversity, abundance, and composition of small rodent species on chronically overgrazed shortgrass rangeland; and 2) to ascertain and explain habitat selection and distribution of particular rodent species across five plant communities typically found on the Edwards Plateau.

CHAPTER 2

METHODS AND MATERIALS

Study Site

The Freeman Ranch is a 1,700-hectare Hill Country ranch located 4.8 km west of San Marcos in Hays County, Texas (N 29°56'18", W 98°00'29"). It is situated on the eastern edge of the Edwards Plateau Ecological Region, the southernmost extension of the Great Plains Physiographic Province (Hunt, 1967), and falls within the Balconian Biotic Province (Blair, 1950). Shallow mollisol soils over Cretaceous limestone rock characterize the region. The eastern edge of the Edwards Plateau is hilly and dissected by streams and steep canyons. Ashe juniper-live oak (*Juniperus ashei-Quercus fusiformis*) woodlands dominate on slopes and in canyons. Uplands are grasslands or savannahs with an interspersion of oak mottes. The encroachment of both Ashe juniper and mesquite (*Prosopis glandulosa*) onto upland sites is evident throughout the Edwards Plateau. Over the last 150 years, the landscape of this region has been altered by human activities, including livestock grazing, suppression of wildfire, and urbanization (Diamond et al., 1987).

The topography of Freeman Ranch is hilly with elevations ranging from 204 to 287 m increasing along a gradient from east to west. Annual mean precipitation ranges from 81 to 91 cm with rainfall peaks in May, June, and September. The average annual temperature is 19.5° C. Predominant soils include those of the Rumple-Comfort association and the Comfort-Rock outcrop complex (USDA Soil Conservation Service, 1984). Rumple and Comfort soils are shallow to moderately deep upland soils, undulating, with a slope of 1 - 8%. Rumple is a cherty clay loam; its surface layer comprises 20% rocks or gravel. Comfort soil is extremely stony clay. Mesquite, Ashe juniper, and Texas persimmon commonly invade soils of the Rumple-Comfort association where overgrazing occurs. The Comfort-Rock outcrop complex consists of shallow, clay soils and rock outcroppings. This soil complex is typically located on slopes and hilltops in upland areas. Horizontal bands of rock outcrop with Comfort soil in between are found on slopes and near drainages. At the surface, up to 45% of Comfort soil is rock. Like the Rumple-Comfort association, soils in this complex are mildly alkaline, well drained, have low water capacity, and a shallow rooting zone. Texas persimmon and Ashe juniper are common invaders where overgrazing occurs. On the Freeman Ranch, the Comfort-Rock outcrop complex roughly follows the contours of the intermittent creek and drainages. At the lowest elevations, where all drainages on the ranch converge, a small patch of Orif soils is found. Orif soils are typically found on floodplains that are intermittently inundated during the year. Soils are deep, and slopes are usually <1%. The surface layer is gravelly loamy sand, about 51 cm deep, with a deep rooting zone. Erosion hazard is high. The Low Stony Hills range site comprises the dominant soil types found on the ranch.

Common woody plants include live oak, honey mesquite, Ashe juniper, cedar elm (*Ulmus crassifolia*), hackberry (*Celtis* sp.), Texas persimmon (*Diospyros texana*), and greenbriar (*Smilax bona-nox*). On upland savannahs, shortgrasses and a variety of forbes dominate the herbaceous community. Important grasses include *Stipa leuchotricha, Bouteloua rigidiseta, Bothriochloa ischaemum,* and *Hilaria belangeri* (Ruiseco and Barnes, unpubl. data, 1998). *Croton* sp. and *Meximalva filipes* are common forbes. Important herbaceous species in lowland, wooded areas are *Sedge* spp., *Calyptocarpus vialis*, and *Stipa leuchotricha.* Based on a recent study of plant communities at Freeman Ranch, the rangeland was rated as "poor" (25% or less of climax vegetation remaining), indicative of chronic overgrazing (Ruiseco and Barnes, unpubl. data, 1998). This classification follows Soil Conservation Service descriptions for range condition classes and the potential plant community for the Low Stony Hills range site (USDA Soil Conservation Service, 1984).

The ranch has been managed by the Agriculture Department of Southwest Texas State University since 1984, and it has a long history of overgrazing. In the past few years, range management practices, including downstocking, rotational grazing, installation of electric fences, and installation of a high fence to manage white-tailed deer, *Odocoileus virginianus,* have been introduced to improve the rangeland (B. Davis, pers. comm.). Inside a high fence area (548 ha), the current stocking rate of cattle is an animal unit/14 ha; on the remainder of the ranch, the stocking rate is an animal unit/10 ha (B. Davis, pers. comm.).

Five study sites, each representing major floral communities of the ranch, were selected. Habitat types were chosen on the basis of plant species composition and vegetative structure. Habitat types included live oak savannah, live oak woodland, mesquite savannah, riparian, and Ashe juniper-live oak forest (Figure 1). Grazing continued throughout the study period. Study sites were sampled after cattle had been

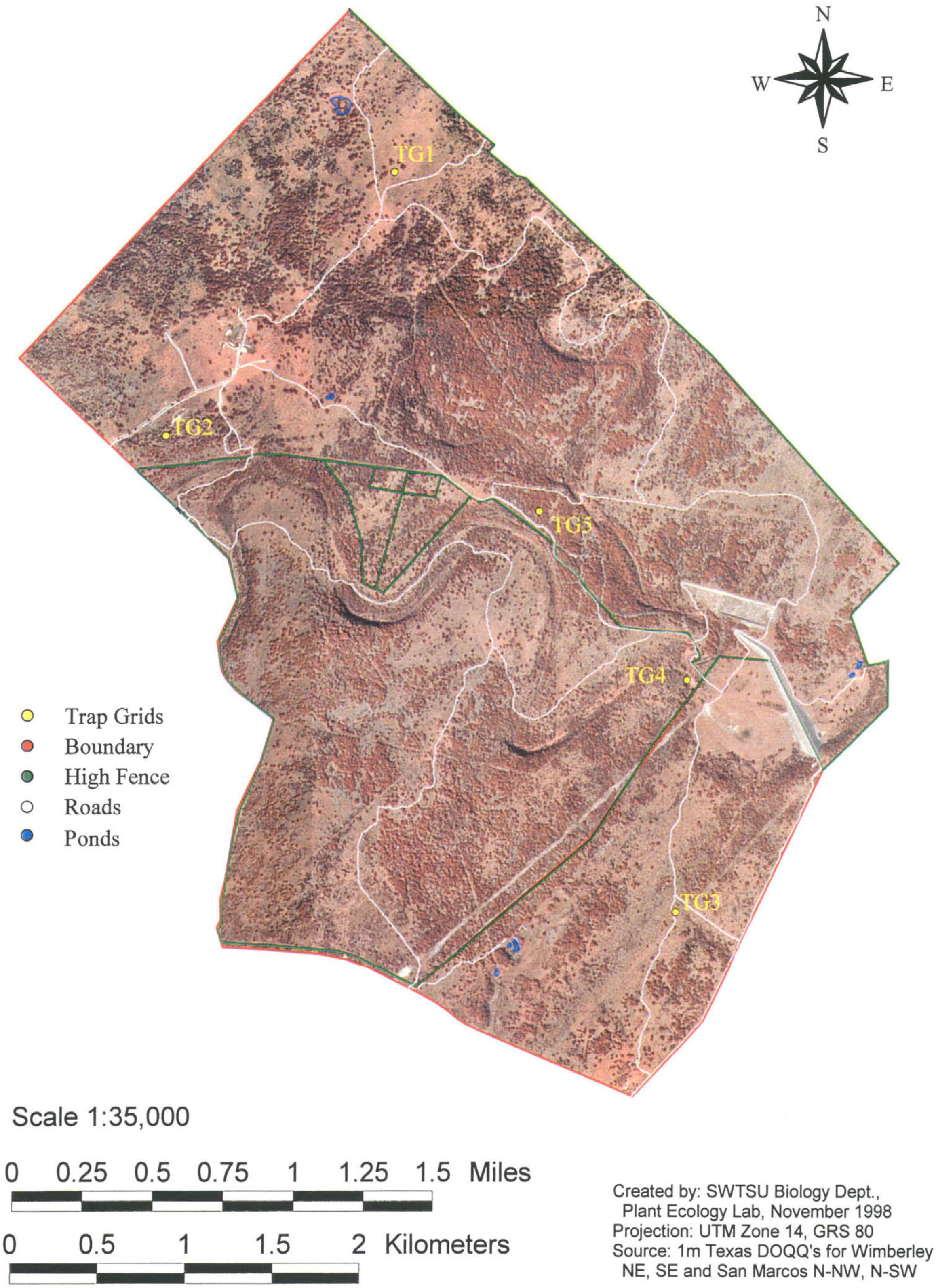


Figure 1. Locations of small rodent trap grids at five habitat types at the Freeman Ranch: live oak savannah (TG1), live oak woodland (TG2), mesquite savannah (TG3), riparian (TG4), and Ashe juniper-live oak forest (TG5).

rotated out of a pasture. The only site where grazing did not occur during this study was the live oak woodland habitat type. Grazing had been curtailed in this area 31 months prior to the study.

Sampling

Vegetation Sampling

In order to describe and compare habitat types selected for rodent sampling, an inventory of woody plants was conducted at each study site by the line-intercept method (Simpson et al., 1996). From these data, relative density, percent cover, dominance, and frequency were calculated for each plant species. Vegetation analysis took place in March, April, and May of 1998, allowing for comparison of different habitats within one season (Nudds, 1977). Five permanent points (T-posts) within each habitat type were established and used as sampling stations. T-posts were randomly placed (at least 250 m apart) within an area of relatively uniform habitat. One line transect, 50 m in length, was extended from each sampling station in a randomly chosen cardinal direction. Canopy and understory species that intercepted the line, or were above or below the line, were recorded, along with their intercept lengths. The taxonomy of woody plants follows Correll and Johnson (1996).

Vertical structure refers to the density of vegetative cover at various heights in the understory (Nudds, 1977). To quantify this feature, a vegetation profile board 2.5 m in height was used. The profile board can be used to estimate the percent of visual obstruction created by vegetation at different heights (Mitchell and Glenn, 1995). Increments of 0.5 m were delineated on the board, and percent of visual obstruction was assigned to one of five classes: 0-20% = 1; 21-40% = 2; 41-60% = 3; 61-80% = 4; and

81-100% = 5 (Nudds, 1977). Four sampling points in the four cardinal directions were used at each sampling station with the T-post as the center point. The board was placed 15 m from the station. The reader estimated the amount of visual obstruction for each height increment. For each habitat type, a total of 20 sampling points were recorded.

Small Rodent Sampling

Between 6 January and 29 March 1998, small rodent populations were systematically sampled in the five habitat types described above. In each habitat, Sherman live traps (23 x 8 x 8 cm) were arranged in a 10,000 m^2 grid with traps aligned in a 10 x 10 trap-station pattern and spaced approximately 10 m apart. To stay within uniform habitat, some grids were broken into two or three adjacent subgrids with a different trap-station pattern. Each habitat type was trapped for 1,500 trap nights with a total trap effort in all habitat types of 7,500 trap nights. Traps were open on consecutive nights, except in the Ashe juniper-live oak forest, where traps were open for six nights, then temporarily closed for 17 nights and reopened again to finish trapping. All traps were baited and refreshed every three days with a combination of rolled oats and birdseed with peanut butter. Rodents were identified and released at point of capture. Taxonomy for small rodents follows Hall (1981).

Data Analysis

Vegetation Analysis

Data derived from the line intercept survey were used to compute relative density, percent cover, dominance, and frequency of woody plants in each habitat type (Cox, 1996). Relative density was calculated as the number of individuals of species (i) divided by the total number of individuals of all species. Percent cover was calculated as the sum of all intercept lengths for species (*i*) divided by total transect length (250 m). Frequency was obtained by dividing the number of 10 m intervals in which species (*i*) occurred by the total number of intervals (n = 25) on the transect. Dominance was calculated by multiplying percent cover by 107,636.76 m^2/ha. A Relative Importance Value (RIV) was calculated for each species by summing relative density, relative frequency, and relative cover values and dividing by three. Species richness was a count of the number of species present in each habitat type.

Vertical structure data was used to construct frequency distribution tables of cover classes for each habitat type. Classes correspond to the percent of visual obstruction created by vegetation at various height increments in the understory. To facilitate comparisons of the vertical arrangement of vegetation, a histogram was generated for each habitat type.

Small Rodent Analysis

Individual species abundances for small rodents were calculated as total number of individuals captured per 100 trap nights (Carey and Johnson, 1995). Species richness was determined by summing the number of species trapped in each habitat type. Because trap effort was equal in all five habitats, species richness values for the five study sites are comparable. Brillouin's index was used to determine community diversity and evenness for each habitat type:

$$\mathrm{H} = (1/N)\log_2\left[\frac{N!}{n_1!n_2!n_3!\ldots}\right]$$

Where

N = total number of individuals of all species in the collection,

n_i = number of individuals belonging to species 1, 2, 3 ....

Like the Shannon-Wiener Index, Brillouins's index (H) measures the degree of uncertainty in predicting into which category a randomly drawn sample from a community will fall (Zar, 1996). The value of H increases with increasing uncertainty (i.e., increasing diversity in a community). The minimum value for H is zero, indicating no uncertainty (i.e., all samples fall into one category). Both diversity measures tend to underestimate actual community diversity, especially with small sample sizes, as rare species are left undetected (Krebs, 1989; Zar, 1996). For the field sampling conducted in this study, the Brillouin Index is a more appropriate measure than the Shannon-Wiener Index, the application of which should be restricted to a large number of random samples drawn from a large community where the total number of species in the community is known (Krebs, 1989). This was not the case in any of the habitat types sampled. The individuals captured in each habitat type can be viewed instead as finite collections.

An evenness statistic (J) was also calculated for each community:

$$J = \frac{H}{H_{max}}$$

Where:

H = observed diversity, based on Brillouin's index,

H_{max} = maximum possible diversity, given sample size N and number of species observed (k).

Evenness statistics measure diversity as a proportion of the maximum possible diversity for a given community. Evenness values range from 0 to 1. A value of 1 indicates that, in the community sample, observations are distributed equally among all categories. The evenness statistic is biased in that it represents an overestimate of equitability (Krebs, 1989; Zar, 1996). That is, if H is an underestimate of diversity, then J must be an overestimate, because H_{max} is based on the number of categories observed ($H_{max} = \log k$, k is the number of categories or species). Therefore, caution should be used when interpreting evenness values. Heterogeneity and evenness measures were derived using the software program DIVERS (Krebs, 1988). Rodent communities were compared across habitat types by calculating total abundance of all species in a habitat, species richness (k), species diversity (H), and evenness (J).

In order to compare small rodent diversity of Freeman Ranch with other study sites, data from all habitat types was pooled, and diversity recalculated using the Shannon-Wiener Index with a logarithmic base of 10. In this way, both a single diversity (H') and a single evenness value (J') was obtained for the entire ranch.

To test for habitat selection, a chi-square value was calculated using raw data for the sample distributions of three of the four species captured across all five habitat types (Holbrook, 1978; Songer et al., 1997). Habitat selection would be supported by a statistically significant difference between the number of individuals captured of species (i) in a given habitat and the expected number captured of this species if it were distributed randomly across all habitats. Because all habitats were sampled equally (time and area covered), expected frequency values were calculated as the total number of individuals (n) of species (i), divided by the number of habitats sampled (k). Thus, the null hypothesis states that the sample distribution of species (i) comes from a population having a trap frequency of n / k. Conversely, the alternate hypothesis states that the sample distribution comes from a population having a trap frequency not equal to n / k. A significant chi-square value indicates that the species is not randomly distributed across habitat types (Holbrook, 1978; Songer et al., 1997). According to Zar (1996), the chi-square test is robust if values meet the following guidelines. One is testing for uniform distribution, i.e., expected frequency = n / k, where n is the sample size, and k is the number of classes or habitats; and in addition, $k \geq 3$, $n \geq 10$, and $n^2 / k \geq 10$. Values for three of the four rodent species captured (*Baiomys taylori, Peromyscus pectoralis,* and *Sigmodon hispidus*) met these criteria. A chi-square test was inappropriate for *Reithrodontomys fulvescens* because of the low sample size.

To ascertain if a significant chi-square value is the result of discrepancies between observed and expected frequencies in certain classes or the result of the observed frequencies in all classes combined, the chi-square analysis can be subdivided (Zar, 1996). In subdividing the analyses for the sample distributions of *P. pectoralis, S. hispidus,* and *B. taylo*ri, relevant habitat types were isolated in the calculations, and new chi-square values were obtained. The Yates correction for continuity was used when degrees of freedom (v) equaled 1 (Zar, 1996). Chi-square table values are based on a continuous distribution, whereas the distribution of possible values from the actual data used is a discrete or discontinuous distribution. A correction becomes necessary only when the number of classes being tested equals two. The Yates correction was made to avoid inflated chi-square values, which would result in an increase in Type I errors (i.e., rejecting the null hypothesis when it should be retained).

CHAPTER 3

RESULTS

Habitat Types

Species compositions of woody plants were remarkably similar from one habitat type to the next, and the same woody plant species dominated all habitat types. However, there were wide discrepancies in the amount of total available cover. Only five species of trees constituted the entire canopy in three of the five habitats: live oak, cedar elm, hackberry, Ashe juniper, and honey mesquite. Excluding mesquite, these same canopy species were also found in the Ashe juniper-live oak forest. In the fifth habitat type, the riparian area, Spanish oak (*Quercus buckleyi*) was present, in addition to the aforementioned species. Greenbriar and Texas persimmon dominated understory vegetation in all habitat types except the Ashe juniper-live oak forest.

Woody plant species richness values ranged from 11 to 16 for four of the habitat types. The fifth habitat type, riparian, had a richness of 25 (Table 1). The riparian community had the highest percent cover (144.8%), as well as the highest density of individual woody plants, while the live oak savannah and mesquite savannah habitat types had the lowest total cover (53.9% and 59.8%, respectively) and the lowest density of individuals (137 and 121, respectively).

There was a high degree of variation in the density of cover at different heights in the understory (vertical structure), both within and between habitat types (Table 2, Fig. 2). In both the mesquite savannah and live oak savannah habitat types, cover class 1

(0-20% visual obstruction) was recorded most often at all height increments in the understory. The riparian community exhibited the greatest variability in vertical

Table 1. Comparison of woody plant communities across five habitat types at the Freeman Ranch, March to May, 1998. Species richness (*k*), total number of individuals (n), total intercept length (m) for all species recorded, and total percent cover of woody plants are given for each habitat type.

Habitat Type	*k*	n	Total intercept Length	Percent Cover
Live Oak Savannah	15	137	134.7	0.54
Live Oak Woodland	15	260	313.4	1.25
Mesquite Savannah	16	121	149.5	0.60
Riparian	25	296	361.9	1.45
Juniper-Oak Forest	11	167	302.9	1.21

structure, especially between 0.0 and 1.5 m. This habitat was the most structurally diverse of all habitat types due to its ecotonal quality. In the Ashe juniper-live oak forest and the live oak woodland habitat types, the distribution of cover classes at all height increments was bimodal.

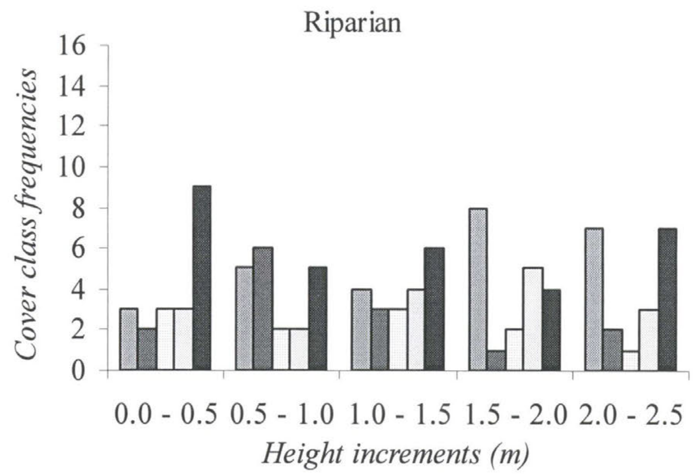
Live Oak Savannah

The woody vegetation of the oak savannah habitat type was dominated by live oak and mesquite (relative cover equals 20.1% and 13.3%, respectively; Table 3). Ashe juniper was also present (9.1% relative cover). The understory was dominated by Texas persimmon saplings and greenbriar (relative cover values of 14.2% and 16.7%, respectively). The total percent cover of all woody plant species was 53.9%. This habitat

Table 2. Frequency distribution of cover classes at five height increments (m) in the understory for five habitat types at the Freeman Ranch, March – May, 1998. Cover classes correspond to percent of visual obstruction created by vegetation: 1 = 0 – 20%, 2 = 21 – 40%, 3 = 41 – 60%, 4 = 61 – 80%, 5 = 81 – 100%.

		Height Increments (m)					
Habitat Type	Class	0.0 – 0.5	0.5 – 1.0	1.0 – 1.5	1.5 – 2.0	2.0 – 2.5	0.0 – 2.5
Live Oak Savannah	1	12	14	13	15	15	69
	2	2	2	3	0	1	8
	3	1	1	1	2	0	5
	4	0	0	0	0	2	2
	5	5	3	3	3	2	16
Live Oak Woodland	1	5	8	11	12	13	49
	2	2	1	0	0	0	3
	3	0	2	0	1	0	3
	4	1	1	1	0	0	3
	5	12	8	8	7	7	42
Mesquite Savannah	1	8	11	14	14	14	61
	2	2	4	1	1	2	10
	3	1	2	1	4	3	11
	4	3	1	2	0	0	6
	5	6	2	2	1	1	12
Riparian	1	3	5	4	8	7	27
	2	2	6	3	1	2	14
	3	3	2	3	2	1	11
	4	3	2	4	5	3	17
	5	9	5	6	4	7	31
Juniper-Oak Forest	1	5	6	7	8	7	33
	2	0	3	0	0	1	4
	3	2	2	1	1	0	6
	4	2	2	3	2	1	10
	5	11	7	9	9	11	47

a.



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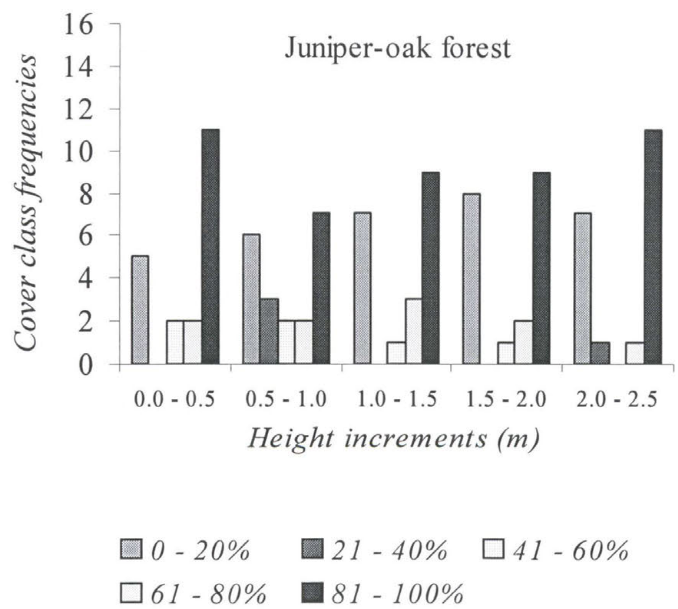
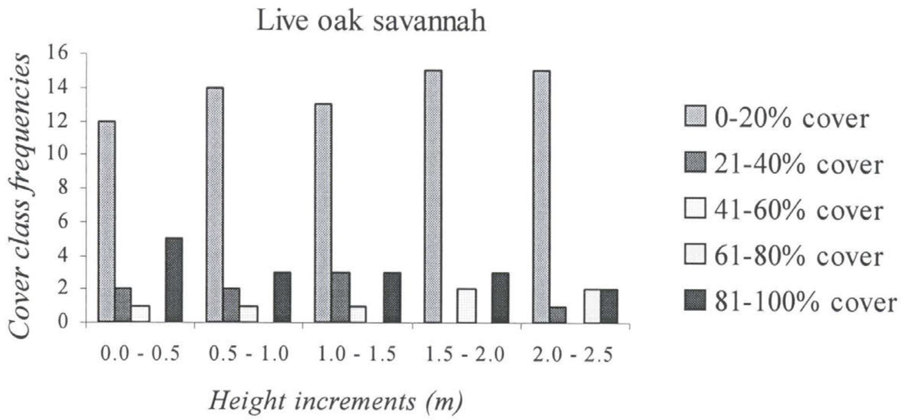


Figure 2. Frequency of cover classes at five height increments in the understory of riparian (a), juniper-oak forest (b), live oak savannah (c), live oak woodland (d), and mesquite savannah (e) habitat types at the Freeman Ranch, March – May, 1998. Classes correspond to percent of visual obstruction created by vegetation (see legend).

Figure 2. continued.

c.



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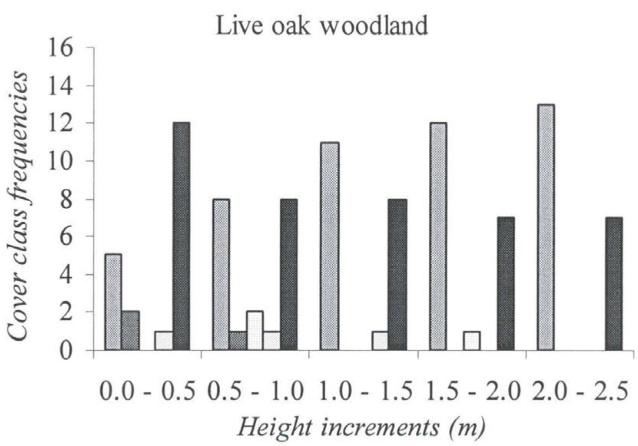
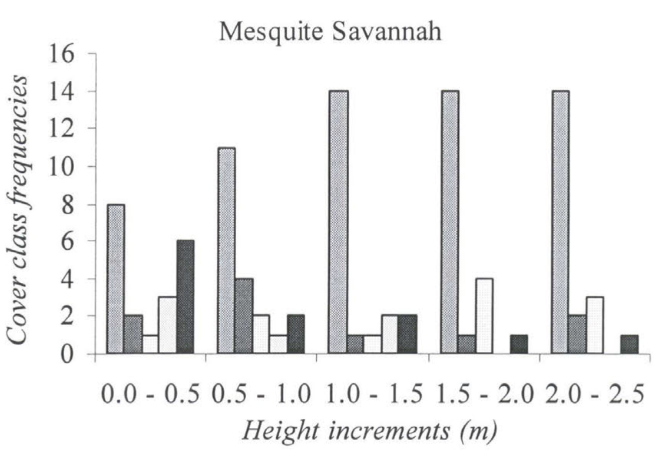


e.



type is an upland savannah interspersed with oak mottes with extensive encroachment by honey mesquite. As expected for savannah habitats, the most frequent cover class for all height increments in the understory was 1, corresponding to 0 – 20% visual obstruction created by vegetation (Fig. 2).

Live Oak Woodland

The live oak woodland habitat type comprised relatively open woodlands juxtaposed with large patches of open grassland where shortgrass and midgrass species dominated (Table 4). Live oak constituted 36.3% relative cover. Ashe juniper was the second most important canopy species with 12.4% relative cover. Common understory species included Texas persimmon, greenbriar, and elbow bush (*Forestiera pubescens*). The patchy landscape probably explains the bimodal distribution of cover classes for vegetation at all heights, with cover class 1 (0 – 20% visual obstruction) recorded most often in grassland areas and cover class 5 (81 – 100% visual obstruction) recorded most frequently in wooded areas (Fig. 2). The total percent cover of 125.4% was twice that of the live oak savannah habitat type.

Mesquite Savannah

Mesquite trees and hackberry saplings dominated the woody plant community in the mesquite savannah habitat type (relative cover values of 23.0% and 18.0%, respectively; Table 5). Important understory species were Texas persimmon and greenbriar, as well as a number of thorny species, such as prickly pear (*Opuntia*

Table 3. Species composition, percent cover, dominance, relative cover, percent frequency, relative frequency and importance values for woody vegetation in the live oak savannah habitat type at the Freeman Ranch, March to May, 1998.

Species	Relative Density	Percent Cover	Dominance (m2/ha)	Relative Cover	Percent Frequency	Relative Frequency	RIV
Trees							
Celtis sp.	0.036	0.003	344.4	0.006	0.20	0.072	0.038
Juniperus ashei	0.073	0.049	5295.7	0.091	0.12	0.043	0.069
Prosopis glandulosa	0.029	0.072	7706.8	0.133	0.24	0.087	0.083
Quercus fusiformis	0.051	0.108	11667.8	0.201	0.16	0.058	0.103
Ulmus crassifolia	0.007	0.012	1291.6	0.022	0.08	0.029	0.020
Shrubs and vines							
Berberis sp.	0.058	0.022	2325.0	0.040	0.20	0.072	0.057
Diospyrus texana	0.109	0.076	8223.4	0.142	0.32	0.116	0.122
Eysenhardtia texana	0.007	0.004	387.5	0.007	0.04	0.014	0.009
Opuntia engelmannii	0.029	0.018	1937.5	0.033	0.12	0.043	0.035
O. leptocaulis	0.051	0.019	2066.6	0.036	0.20	0.072	0.053
Forestiera pubescens	0.051	0.017	1851.4	0.032	0.12	0.043	0.042
Parthenocissus quinquefolia	0.109	0.026	2841.6	0.049	0.24	0.087	0.082
Rubus trivialis	0.080	0.015	1593.0	0.027	0.16	0.058	0.055
Smilax bona-nox	0.277	0.090	9687.3	0.167	0.48	0.174	0.206
Vitis sp.	0.029	0.007	775.0	0.013	0.08	0.029	0.024
Total	1.000	0.539	57994.7	1.000	2.76	1.000	1.000

Table 4. Species composition, percent cover, dominance, relative cover, percent frequency, relative frequency and importance values for woody vegetation in the live oak woodland habitat type at the Freeman Ranch, March to May, 1998.

Species	Relative Density	Percent Cover	Dominance (m2/ha)	Relative Cover	Percent Frequency	Relative Frequency	RIV
Trees							
Celtis sp.	0.069	0.035	3788.8	0.028	0.40	0.078	0.058
Juniperus ashei	0.100	0.155	16705.2	0.124	0.48	0.094	0.106
Prosopis glandulosa	0.004	0.024	2540.2	0.019	0.04	0.008	0.010
Quercus fusiformis	0.119	0.455	48953.2	0.363	0.68	0.133	0.205
Ulmus crassifolia	0.065	0.036	3918.0	0.029	0.28	0.055	0.050
Shrubs and vines							
Berberis sp.	0.054	0.050	5381.8	0.040	0.40	0.078	0.057
Bumelia lanuginosa	0.038	0.014	1463.9	0.011	0.20	0.039	0.029
Diospyrus texana	0.123	0.148	15973.3	0.118	0.64	0.125	0.122
Forestiera pubescens	0.050	0.087	9342.9	0.069	0.28	0.055	0.058
Parthenocissus quinquefolia	0.046	0.017	1851.4	0.014	0.24	0.047	0.036
Rubus trivialis	0.065	0.016	1722.2	0.013	0.36	0.070	0.049
Smilax bona-nox	0.235	0.195	21010.7	0.156	0.88	0.172	0.187
Toxicodendren radicans	0.008	0.001	86.1	0.001	0.08	0.016	0.008
Vitis sp.	0.008	0.011	1205.5	0.009	0.12	0.023	0.013
Yucca rupicola	0.015	0.009	990.3	0.007	0.04	0.008	0.010
Total	1.000	1.254	134933.4	1.000	5.12	1.000	1.000

engelmannii), agarita (*Berberis* sp.), and tasajillo (*O. leptocaulis*). Vegetative cover was fairly sparse (59.8%) compared to other habitat types.

As with the live oak savannah habitat type, cover class 1 (0 – 20% visual obstruction) was the most frequent value recorded at all height increments in the understory (Fig. 2). However, for the increment 0.0 – 0.5 m, the distribution of cover classes for the mesquite savannah was slightly skewed to higher cover classes, reflecting the abundance and interspersion of low shrubs.

Riparian

The riparian habitat type is a lowland forest dominated by Ashe juniper, cedar elm, and live oak (Table 6). Other canopy species included hackberry, Spanish oak, and mesquite. Greenbriar and Texas persimmon dominated the understory. *Vitis* sp. and elbow bush were also important understory components. Species richness ($k = 25$), total percent cover (144.8%), and the density of woody plants (296) were higher in the riparian area than in any other habitat type.

The riparian area exhibited the greatest heterogeneity in vegetative structure of all habitat types sampled. At the lowest elevations, where Orif soils occur and flooding potential is high, woody vegetation was absent. Elsewhere, limestone bluffs and dense woody vegetation characterized the landscape along narrow creek drainages. The creek bed along a north-facing bluff supported a compositionally diverse understory and canopy, presumably due to higher available moisture. In one area, large live oaks were found with no understory development, and at slightly higher elevations, dense

Table 5. Species composition, percent cover, dominance, relative cover, percent frequency, relative frequency and importance values for woody vegetation in the mesquite savannah habitat type at the Freeman Ranch, March to May, 1998.

Species	Relative Density	Percent Cover	Dominance (m2/ha)	Relative Cover	Percent Frequency	Relative Frequency	RIV
Trees							
Celtis sp.	0.107	0.108	11581.7	0.180	0.44	0.133	0.140
Juniperus ashei	0.050	0.039	4219.4	0.066	0.20	0.060	0.058
Prosopis glandulosa	0.132	0.138	14810.8	0.230	0.48	0.145	0.169
Quercus fusiformis	0.008	0.016	1722.2	0.027	0.04	0.012	0.016
Ulmus crassifolia	0.091	0.033	3573.5	0.056	0.28	0.084	0.077
Shrubs and vines							
Acacia farnesiana	0.008	0.006	645.8	0.010	0.04	0.012	0.010
Berberis sp.	0.074	0.042	4563.8	0.071	0.24	0.072	0.073
Bumelia lanuginosa	0.017	0.002	258.3	0.004	0.08	0.024	0.015
Cercis canadensis	0.008	0.001	86.1	0.001	0.04	0.012	0.007
Colubrina texensis	0.008	0.002	258.3	0.004	0.04	0.012	0.008
Condalia hookeri	0.017	0.010	1119.4	0.017	0.08	0.024	0.019
Diospyrus texana	0.132	0.065	6974.9	0.108	0.28	0.084	0.108
Forestiera pubescens	0.050	0.012	1334.7	0.021	0.16	0.048	0.040
Opuntia engelmannii	0.182	0.047	5037.4	0.078	0.44	0.133	0.131
Opuntia leptocaulis	0.041	0.020	2109.7	0.033	0.16	0.048	0.041
Smilax bona-nox	0.074	0.056	6070.7	0.094	0.32	0.096	0.088
Total	1.000	0.598	64366.8	1.000	3.32	1.000	1.000

Table 6. Species composition, percent cover, dominance, relative cover, percent frequency, relative frequency and importance values for woody vegetation in the riparian habitat type at the Freeman Ranch, March to May, 1998.

Species	Relative Density	Percent Cover	Dominance (m2/ha)	Relative Cover	Percent Frequency	Relative Frequency	RIV
Trees							
Celtis sp.	0.047	0.058	6242.9	0.040	0.40	0.074	0.054
Juniperus ashei	0.189	0.300	32334.1	0.208	0.64	0.118	0.171
Prosopis glandulosa	0.017	0.023	2454.1	0.016	0.08	0.015	0.016
Quercus fusiformis	0.034	0.274	29449.4	0.189	0.40	0.074	0.099
Q. buckleyi	0.030	0.030	3229.1	0.021	0.12	0.022	0.024
Ulmus crassifolia	0.149	0.284	30568.8	0.196	0.68	0.125	0.157
Shrubs and vines							
Baccharis neglecta	0.003	0.002	258.3	0.002	0.04	0.007	0.004
Berberis sp.	0.010	0.005	559.7	0.004	0.08	0.015	0.009
Bernardia myricifolia	0.007	0.003	344.4	0.002	0.08	0.015	0.008
Bumelia lanuginosa	0.003	0.001	86.1	0.001	0.04	0.007	0.004
Ehretia anacua	0.003	0.004	473.6	0.003	0.04	0.007	0.005
Diospyrus texana	0.088	0.122	13174.7	0.085	0.44	0.081	0.084
Forestiera pubescens	0.047	0.040	4262.4	0.027	0.20	0.037	0.037
Ilex decidua	0.020	0.020	2195.8	0.014	0.24	0.044	0.026
I. vomitoria	0.003	0.002	172.2	0.001	0.04	0.007	0.004
Juglans sp.	0.014	0.038	4047.1	0.026	0.16	0.029	0.023
Mimosa borealis	0.003	0.004	387.5	0.002	0.04	0.007	0.004
Opuntia engelmannii	0.007	0.006	602.8	0.004	0.04	0.007	0.006
O. leptocaulis	0.010	0.004	387.5	0.002	0.12	0.022	0.012
Parthenocissus quinquefolia	0.014	0.004	473.6	0.003	0.12	0.022	0.013
Ptelea trifoliata	0.003	0.000	43.1	0.000	0.04	0.007	0.004
Rubus trivialis	0.061	0.016	1765.2	0.011	0.36	0.066	0.046
Smilax bona-nox	0.166	0.105	11323.4	0.073	0.60	0.110	0.116
Ungnadia speciosa	0.030	0.028	3013.8	0.019	0.16	0.029	0.026
Vitis sp.	0.041	0.074	7965.1	0.051	0.28	0.051	0.048
Total	1.000	1.448	155815.0	1.000	5.44	1.000	1.000

associations of large cedar elms, hackberries, and live oaks occurred. This heterogeneity was reflected in measures of vertical structure (Fig. 2). The distribution of cover classes for understory vegetation was highly variable and there was no obvious overall pattern.

Ashe juniper-Live oak Forest

The Ashe juniper-live oak forest was dominated by two species (Ashe juniper 51.5% of relative cover, live oak 32%; Table 7). Cedar elm was less common (7.3% relative cover). Understory species constituted only 7.2% of woody vegetation. Greenbriar and Texas persimmon (1.2% and 2.2% relative cover, respectively) were found in the closed, densely forested areas dominated by junipers. In the small, enclosed pockets of open grassland, prickly pear was the dominant woody plant (3.2% relative cover). Total percent cover for woody vegetation was 121.2%. Species richness was 11. As with the live oak woodland habitat type, the bimodal distribution of cover classes for understory vegetation can be explained by the patchiness of this habitat. Open patches had 0 –20% vegetative cover at all heights, while densely forest areas had 81 – 100% vegetative cover at all height increments.

Small Rodent Results

A total of 149 *Peromyscus pectoralis*, 44 *Sigmodon hispidus*, 19 *Baiomys taylori*, and 1 *Reithrodontomys fulvescens* were captured during the study. Individual species abundances (Carey and Johnson, 1995), as well as total abundance of small rodents for each habitat type, are presented in Table 8. The Ashe juniper-live oak forest had the

Table 7. Species composition, percent cover, dominance, relative cover, percent frequency, relative frequency and importance values for woody vegetation in the Ashe juniper-live oak forest habitat type at the Freeman Ranch, March to May, 1998.

Species	Relative Density	Percent Cover	Dominance (m2/ha)	Relative Cover	Percent Frequency	Relative Frequency	RIV
Trees							
Celtis sp.	0.012	0.018	1894.4	0.015	0.08	0.033	0.020
Juniperus ashei	0.581	0.624	67208.4	0.515	0.84	0.350	0.482
Quercus fusiformis	0.186	0.396	42581.1	0.327	0.64	0.267	0.260
Ulmus crassifolia	0.042	0.088	9472.0	0.073	0.20	0.083	0.066
Shrubs and vines							
Condalia hookeri	0.006	0.000	43.1	0.000	0.04	0.017	0.008
Diospyrus texana	0.030	0.026	2841.6	0.022	0.12	0.050	0.034
Forestiera pubescens	0.006	0.004	387.5	0.003	0.04	0.017	0.009
Opuntia engelmannii	0.066	0.038	4133.3	0.032	0.16	0.067	0.055
Opuntia leptocaulis	0.006	0.001	129.2	0.001	0.04	0.017	0.008
Smilax bona-nox	0.060	0.014	1506.9	0.012	0.20	0.083	0.052
Yucca rupicola	0.006	0.002	215.3	0.002	0.04	0.017	0.008
Total	1.000	1.212	130412.7	1.000	2.40	1.000	1.000

highest total abundance of small rodents (5.27 individuals captured/100 trap nights), whereas the riparian forest had the lowest total abundance (0.94). The mean total abundance for all five habitat types was 2.85 individuals/100 trap nights.

The highest species richness ($k = 4$) occurred in the mesquite savannah habitat type (Table 9). This was the only habitat type in which *Reithrodontomys fulvescens* occurred. *Peromyscus pectoralis* was the only species trapped in the Ashe juniper-live oak forest. This habitat type had the lowest species richness ($k = 1$).

Diversity of small rodents in the five habitat types ranged from 0.00 to 1.37 (Table 9). The live oak savannah had both the highest diversity value and the highest evenness value. The mesquite savannah also had high diversity (1.33), but a low evenness value. The Ashe juniper-live oak forest habitat type had the lowest diversity (0.00), as only *P. pectoralis* was caught. Evenness for this community was also 0.00.

Frequency of captures across the five habitat types was significantly different from what would be expected due to random chance for *Peromyscus pectoralis* ($\chi^2 = 108.6$, d.f. = 4, $P < 0.001$), *Baiomys taylori* ($\chi^2 = 18.1$, d.f. = 4, $0.001 < P < 0.005$), and *Sigmodon hispidus* ($\chi^2 = 24.6$, d.f. = 4, $P < 0.001$). There was a significant non-random association of the white-ankled mouse, *Peromyscus pectoralis*, and the Ashe juniper-live oak forest habitat type ($\chi^2_{0.01,1} = 81.7$). The relative paucity of the white-ankled mouse in the riparian forest and live oak savannah habitat types was also significant ($\chi^2_{0.01,1} = 15.9$; $\chi^2_{0.01,1} = 11.0$, respectively). The frequency of captures of the white-ankled mouse in the live oak woodland and mesquite savannah habitat types was not significantly different from what would be expected due to chance.

Table 8. Individual species abundances of small rodents for five habitat types at the Freeman Ranch, Jan. – March, 1998. Abundance equals individuals captured per 100 trap nights. Total sample size (n) of each species is given. Species sample size for each habitat type follows in parentheses. Trap effort for each habitat type equaled 1500 trap nights.

		Habitat Types				
Species	n	Live Oak Savannah	Live Oak Woodland	Mesquite Savannah	Riparian	Juniper-Live Oak Forest
B. taylori	19	0.67(10)	0.34(5)	0.27(4)		
P. pectoralis	149	0.87(13)	1.87(28)	1.34(20)	0.60(9)	5.27(79)
R. fulvescens	1			0.07(1)		
S. hispidus	44	0.47(7)	0.87(13)	1.27(19)	0.34(5)	
Total abundance		2.01	3.08	2.95	0.94	5.27

Table 9. Small rodent species richness, species diversity, and evenness for five habitat types at the Freeman Ranch, January to March, 1998. Species diversity and evenness were calculated using Brillouin's index ($\log_2$).

Habitat Types	Species Richness	Species Diversity	Evenness
Live Oak Savannah	3	1.369	0.970
Live Oak Woodland	3	1.183	0.812
Mesquite Savannah	4	1.327	0.732
Riparian	2	0.783	0.934
Juniper-Live Oak Forest	1	0.000	0.000

There was a significant non-random association between *B. taylori* and the live oak savannah habitat type ($\chi^2_{0.01,1} = 10.7$). The observed frequency of captures of *B. taylori* in all other habitat types was not significantly different from the expected frequency of captures. The observed frequency of captures of *Sigmodon hispidus* in the mesquite savannah habitat type ($\chi^2_{0.001,1} = 10.7$) and in the Ashe juniper-live oak forest habitat type ($\chi^2_{0.01,1} = 7.9$) differed significantly from expected frequency. Live oak woodland, riparian, and live oak savannah habitat types were not significant factors affecting the test statistic for this species.

CHAPTER 4

DISCUSSION

Based on the sampling design employed in this study, four species of small rodents occur on the Freeman Ranch: *Peromyscus pectoralis, Sigmodon hispidus, Baiomys taylori,* and *Reithrodontomys fulvescens*. One species, the fulvous harvest mouse, was unique to a single habitat; it occurred only in the mesquite savannah habitat type. In contrast, the white-ankled mouse was found in all five habitats and was the most abundant rodent species in each, accounting for 70% of all captures.

Savannah habitats (mesquite and live oak) had higher small rodent diversity than woodland or forest habitats. Similar results were reported in two contemporary studies of small rodent diversity on the Edwards Plateau in Lampasas/San Saba Counties and Edwards/Kinney Counties (Table 10) (Schwertner, 1996; Schwausch, 1997). An exception is the river riparian habitat studied by Schwausch (1997) which had a diversity value comparable to grassland habitats.

On the Freeman Ranch, the mesquite savannah habitat type had the highest rodent species richness of all habitats sampled. All four small rodent species found on the ranch occurred here. This habitat type also had the second highest diversity and relatively high small rodent abundance. Thorny scrub species offered concealment for cotton rats, while pygmy mice were caught in open areas with very sparse cover. White-ankled mice were found near clumps of vegetation that always included Ashe juniper, and the single harvest

Table 10. A comparison of small rodent diversity in grassland/savannah habitats and woodland/shrubland habitats. Sampling was conducted at Kickapoo Caverns State Park in Edwards and Kinney counties, 1994-1995; Colorado Bend State Park in San Saba and Lampasas counties, 1995-1996; and the Freeman Ranch, Hays county, 1998. Diversity values (H') are derived using the Shannon-Wiener Index ($\log_{10}$).

Habitat Types	Kickapoo Caverns SP	H'	Colorado Bend SP	H'	Freeman Ranch	H'
Grassland/savannah	King Ranch bluestem	0.38	King Ranch bluestem	0.41	Live oak savannah	0.46
	Little bluestem	0.24	Stipa grassland	0.20	Mesquite savannah	0.45
	Sparse grassland	0.14				
	Intermediate grassland	0.51				
	Dense grassland	0.36				
Shrubland/woodland	Creek riparian	0.00	Creek riparian	0.00	Creek riparian	0.28
	Vasey oak association	0.00	Oak-juniper woodland	0.11	Live oak woodland	0.39
	Pine-oak-juniper woodland	0.00	Juniper forest	0.00	Juniper-oak forest	0.00
	Guajillo shrubland	0.11	River riparian	0.21		
	Mixed brushland	0.15	Oak-persimmon-cactus scrub	0.00		

mouse was trapped in an area with denser, overgrown, woody vegetation along a barbed wire fence. Although all four rodent species occurred in this habitat type, diversity was not the highest in this habitat type due to the low number of captures of *B. taylori* and *R. fulvescens.*

The live oak savannah habitat type had the highest diversity of all habitat types and high species richness, but far fewer captures than the mesquite savannah habitat type. Diversity was the highest of any habitat type, in part because captures were fairly evenly distributed among species categories. Low cover may have limited small rodent abundance. Captures of *P. pectoralis* were restricted to oak mottes that were widely scattered throughout the study site. Cotton rats were trapped near large clumps of thorny vegetation. Pygmy mice were more abundant in this habitat type than in any other and were often trapped out in the open, in sparse grass, far from any other cover.

The riparian habitat type had the second lowest diversity value and the lowest total abundance of any habitat type. In addition, of the two species present, *P. pectoralis* and *S. hispidus*, the latter was entirely localized to a man-made brush pile, which provided more cover than would otherwise have been available in this habitat. Other studies have found cotton rats to be absent from creek riparian habitats elsewhere on the Edwards Plateau (Schwertner, 1996; Schwausch, 1997).

The Ashe juniper-live oak forest habitat type was unique in that only one rodent species occurred here. However, it also supported the greatest abundance of small rodents.

The live oak woodland habitat type had a relatively high diversity and species richness compared to other habitats. Species richness and species composition were the same as in the live oak savannah habitat type. However, captures of rodents were less evenly distributed in the live oak woodland habitat. Diversity and evenness values for the two habitats reflect these differences in equitability. Total small rodent abundance for the live oak woodland habitat type was similar to the mesquite savannah habitat type. Only the juniper-oak forest had a higher abundance of small rodents.

Vegetative features and small rodent community characteristics

Analysis of the vegetative characteristics of each habitat type indicate that the overall amount of vegetative cover and the species richness of woody plants are not good predictors of species abundance of small rodents or diversity. Other habitat features apparently play a more important role. The habitat type with the lowest richness in woody plant species, the Ashe juniper-live oak forest, had the highest abundance of small rodents. On the other hand, it also had the lowest small rodent diversity. The riparian habitat type had the highest species richness of woody plants and the most available cover; notwithstanding, it had the lowest abundance of rodents, low rodent species richness, and low rodent diversity.

The amount of available cover 0.0 – 1.0 m above the ground seems to plays a more important role in determining small rodent faunal characteristics than overall cover or plant species richness and vegetative composition. Although overall available cover was relatively low in the mesquite savannah habitat type, shortgrasses provided cover near to the ground, as did thorny shrubs, especially tasajillo and prickly pear. Compared to the other four habitat types, small rodent abundance was relatively high.

Thorny scrub species may be the reason for the abundance of cotton rats in the mesquite savannah habitat type. Cattle are unable to graze thorny shrubs too closely; thus, dense patches of grasses grow in and around their bases, providing concealment and escape cover from predators. Cotton rats, and occasionally pygmy mice, were also trapped in similar locations in the live oak savannah habitat type, although the abundance of thorny shrubs is less.

The patchiness of the landscape may explain the high diversity, abundance, and richness of small rodents in the live oak woodland habitat type. Open woodlands are juxtaposed with large patches of grassland with transition zones at varying stages of seral development. Open grassland areas support shortgrass and midgrass species. The population of cotton rats in this habitat type was localized to a large, dense patch of midgrass that had flourished in the absence of grazing. This patchiness, as well as curtailed grazing, may well have influenced the diversity of small rodents in this habitat type.

One might expect a similar diversity value for the Ashe juniper-live oak forest habitat type, which is also characterized by patchy vegetation. However, there is little transition between forested and open areas. Small interspersed pockets of open grassland are completely enclosed on all sides by a dense wall of junipers and live oaks. This arrangement probably precludes colonization by *Baiomys taylori*, otherwise found in open grassland areas on the ranch. Furthermore, grazing has reduced the amount of herbaceous vegetation in this habitat type such that sufficient cover for larger rodents is lacking.

Habitat selection

Peromyscus pectoralis, Sigmodon hispidus, and *Baiomys taylori* were non-randomly distributed across the landscape, exhibiting differential use of available habitats. Not surprisingly, the white-ankled mouse selected for the Ashe juniper-live oak forest habitat type. Throughout its distribution, the white-ankled mouse is associated with a variety of rocky environments (King, 1968). On the Edwards Plateau, the white-ankled mouse is often found in rocky, oak-juniper woodlands (Davis and Schmidly, 1994). Baccus and Horton (1984) found this species to be highly correlated with ledges, slopes, and brushpiles. Ledges and brushpiles were used for escape, while 26.6% of the mice observed were noted to climb juniper or oak trees upon release. Thus, the distribution of *P. pectoralis* was highly correlated with habitat features that provided a means of escape or could be used as escape cover.

On the Freeman Ranch, the white-ankled mouse was always trapped near Ashe juniper trees, which are found in all habitat types. It is not clear if *P. pectoralis* is responding to juniper trees or some covariate. It was noted during this field study that *P. pectoralis* is an agile climber and frequently used juniper trees for escape. Its diet includes juniper berries, as well as seeds and insects (Davis and Schmidly, 1994). Another structural feature that *P. pectoralis* may be selecting for is the rockiness of the substrate. The three habitat types where the white-ankled mouse was most abundant were all dominated by soils of the Comfort-Rock outcrop complex, where rock outcroppings alternate with Comfort soils, which comprise up to 45% rock.

Peromyscus pectoralis also showed habitat avoidance of the riparian and live oak savannah habitat types. In the riparian area, only 0.60 individuals per 100 trap nights were captured. This is relatively low compared to 13.7 white-ankled mice per 100 trap nights at the creek riparian habitat at Colorado Bend State Park (Schwausch, 1997) and 7.4 individuals per 100 trap nights at a creek riparian habitat at Kickapoo Caverns State Park (Schwertner, 1996). Reasons for avoidance of this habitat type at the Freeman Ranch by the white-ankled mouse are unclear. However, the low abundance of small rodents may be explained by the impact of heavy grazing, a conclusion supported by Schulz and Leininger (1991). In the live oak savannah habitat type, *P. pectoralis* was captured only in or at the edge of oak mottes that were widely scattered, hence the relative paucity of white-ankled mice in this habitat type.

The distribution of *Sigmodon hispidus* showed strong selection for the mesquite savannah habitat type. This larger rodent is usually found in tallgrass habitats that provide an ample food supply and enough cover for concealment. In the absence of tallgrasses, cotton rats will form dens at the base of low clumps of thorny plant species (Davis and Schmidly, 1994). On the Freeman Ranch, where shortgrasses dominate and grazing reduces available cover, thorny shrubs provided the necessary cover. Thorny shrubs were most abundant in the mesquite savannah habitat type.

As expected, *S. hispidus,* a grassland-adapted species, avoided the densely forested Ashe juniper-live oak habitat type. A lack of sufficient cover probably precludes its colonization of the interspersed, grassy patches.

Baiomys taylori revealed strong selection for the live oak savannah habitat type. Shortgrass species predominate on upland savannahs on the ranch, and pygmy mice seem well adapted to the sparse cover conditions. *B. taylori* was frequently trapped amid closely grazed shortgrasses with little or no other cover nearby in all habitat types where it occurred. At Colorado Bend State Park, the pygmy mouse was also most abundant in a shortgrass habitat dominated by *Stipa* sp. It was less common in the grassland habitat dominated by King Ranch bluestem, a midgrass species (Schwausch, 1997).

Diversity and abundance of small rodents at Freeman Ranch

In their study of North American grasslands and small mammal community characteristics, Grant and Birney (1979) delineated the ecological patterns in the geographic distribution of small mammal grassland faunas and compared these ecological patterns with the structural attributes of different grassland types. They concluded that the amount of available cover (aboveground plant biomass) explains to a high degree small mammal faunal characteristics for these ecosystems. They grouped nine grassland types into three broad categories based on available cover: those with high cover (characteristic of midgrass and tallgrass prairies), those with intermediate cover (characteristic of southern shortgrass prairies), and those having low cover (bunchgrass or desert grasslands).

Small mammal faunal communities at grassland sites with high cover were characterized by high total small mammal biomass, low faunal diversity, and litter-dwelling herbivores. Sites with intermediate cover conditions had low total small mammal biomass, low faunal diversity and consisted mainly of surface-dwelling omnivores. Grasslands with low cover had high small mammal biomass, high diversity, and specialized, surface-dwelling granivores. Thus, there was no simple trend in small mammal diversity or evenness as aboveground plant biomass decreased from one grassland type to the next.

According to this paradigm, shortgrass prairies of the Edwards Plateau would have low small mammal diversity with a few opportunistic, omnivorous species. A comparison of diversity at the Freeman Ranch with a range of grassland types surveyed by Grant and Birney (1979) reveals that small mammal diversity is much lower at the Freeman Ranch than at any other grassland site, including a comparable southern shortgrass prairie (Table 11). A diversity value of 0.35 for the ranch falls well outside the range of diversity values (0.66 -1.24) for all other grasslands. An evenness value of 0.59, however, is within the range of values (0.42 – 0.81) for the nine grassland types included in Table 11. The southern shortgrass site in Table 11 is an association of *Bouteloua gracilis* and *Aristida longiseta.* The study site was located in Carson County, Texas, in the High Plains Vegetative Region, where average annual precipitation ranges from 50 to 61 cm. A diversity value of 1.06 for this grassland is well above that derived for the Freeman Ranch. All diversity values from Grant and Birney (1979) are based on sampling of small mammals at ungrazed grassland sites.

There are a number of limitations to this comparison. Sampling intensities and methods were not replicated in the Freeman Ranch study. In addition, Grant and Birney (1979) sampled insectivores as well as rodents, whereas Freeman Ranch diversity values are based on sampling of the small rodent community only, with no captures of insectivores. Finally, wooded and forested habitats, which tend to have a lower small rodent diversity than savannah or grassland habitats (see Table 10) were pooled with savannah habitats to arrive at a single H' value for the Ranch. Sampling sites in Grant and Birney (1979), on the other hand, were restricted solely to representative grassland habitats.

Keeping these disparities in mind, one may ask whether lower diversity at the Freeman Ranch is simply characteristic of grasslands of the Edwards Plateau or if some

Table 11. Comparison of small rodent diversity at the Freeman Ranch, a southern shortgrass grassland type, with other grassland types of North America. Aboveground plant biomass is given, along with diversity (H') and evenness (J') values. North American grassland data adapted from Grant and Birney (1979). H' and J' were derived using the Shannon-Wiener Index ($\log_{10}$).

Grassland type	Aboveground plant biomass (g dry weight/m^2)	Diversity (H')	Evenness (J')
Freeman Ranch			
Southern shortgrass	--	0.35	0.59
North American grasslands			
Bunchgrass	225	0.66	0.53
Montane	300	0.75	0.73
Northern Tallgrass	--	0.84	0.65
Southern Tallgrass	850	0.75	0.42
Northern midgrass	900	0.76	0.54
Southern midgrass	600	0.78	0.81
Northern shortgrass	275	0.90	0.75
Southern shortgrass	475	1.06	0.65
Desert grassland	150	1.24	0.78

other factor, or combination of factors, is impacting small rodent diversity. A study of small rodent community characteristics conducted at the Colorado Bend State Park

(CBSP) offers an apt comparison (Schwausch, 1997). CBSP is also located on the Edwards Plateau, and both sites are similar in terms of plant communities and small rodent species composition. Grazing at CBSP was curtailed nine years prior to the study. Notwithstanding curtailed grazing, diversity measures indicate that CBSP had a lower small rodent diversity than the Freeman Ranch for three comparable habitat types (Table 12). These differences may or may not be significant. Comparison of diversity values is limited for several reasons. First of all, sampling intensities, which do affect H' values, were not the same in the two studies or for all habitat types sampled at CBSP. In addition, rodent sampling at the Freeman Ranch was conducted within one season (January – March), whereas at CBSP, sampling was conducted randomly throughout an entire year. Given these dissimilarities in methods and the fact that rodent populations fluctuate widely from season to season, no firm conclusions can be drawn from these data. Finally, nine years may be an insignificant amount of time for a rangeland with a history of chronic overgrazing to recover, much less for the small rodent fauna dependent on that rangeland.

A comparison of small rodent abundance data for the Freeman Ranch and CBSP reveals the opposite trend of diversity: mean small rodent abundance for all habitat types at Colorado Bend SP was much higher (7.33 individuals/100 trap nights) than at the Freeman Ranch (2.84 individuals/100 trap nights; Table 12). Species richness was slightly higher at CBSP, as well ($k = 5$ at CBSP; $k = 4$ at Freeman Ranch). For two out of three comparable habitat types, abundance was much higher at Colorado Bend SP than at the Freeman Ranch. For the third habitat type, a live oak-juniper woodland, abundance was only slightly higher at the Freeman Ranch (Table 12). Because sampling times were different in the two studies, seasonality is a factor affecting abundance results. Thus, even comparisons between similar habitat types are limited. Differences may or may not be significant.

Table 12. A comparison of small rodent community characteristics at two sites on the Edwards Plateau: Freeman Ranch, Hays County, January through March, 1998; and Colorado Bend State Park (CBSP), Lampasas County, 1995 to 1996. Sampling intensity (trap nights), diversity (H'), and abundance (individuals captured/100 trap nights) are given for three comparable habitat types.

Habitat Type	Site	Trap nights	Diversity (H')	Abundance
Stipa grassland/	Freeman Ranch	1,500	0.46	2.01
savannah	CBSP	540	0.20	10.00
Riparian (creek)	Freeman Ranch	1,500	0.28	0.94
	CBSP	168	0.00	13.7
Live oak-juniper	Freeman Ranch	1,500	0.39	3.08
woodland	CBSP	1,108	0.11	2.71

That small rodent abundance may be negatively affected by intensive grazing is a conclusion supported by Rosenstock (1996) in his study of semi-arid grasslands. Chronic overgrazing reduces potential cover, and as ground cover is removed, soils tend to loose moisture more rapidly, and desertification of rangeland can occur. Increased aridity leads to a decrease in primary productivity and finally, to a decreasing food supply for herbivores. Grant and Birney (1979) suggested that the key element linking aboveground plant biomass and small mammal faunal characteristics in grasslands is the food supply. For example, at grassland sites with intermediate cover, characteristic of southern shortgrass prairies, both herbage and seed supplies are marginal. This situation favors only a few generalist species. Leaf-litter is likewise minimal, precluding habitat utilization by litter-dwellers. The minimal quantity and quality of the food supply results in low small mammal biomass. In this scenario, then, the effect of overgrazing would be to further reduce a food supply that is already marginal to begin with.

Future research

Given the functional role of small rodent populations in grassland ecosystems, decreasing abundance cannot but impact the structure of the native biotic community. Still, caution must be used when interpreting diversity or abundance data as ecological indicators of the health of a community. Populations of small rodents are extremely volatile, both spatially and temporally (Rosenstock, 1996). Shortgrass prairies in particular are highly variable from season to season in terms of total small mammal biomass (Grant et al., 1982). Thus, the findings of one study are limited in themselves, but can be interpreted within a larger research context.

Research conclusions on the effects of grazing on small rodent communities on shortgrass prairies are far from unanimous. Experimental results are often contradictory. Grant et al. (1982) found no significant difference in small mammal diversity on lightly versus heavily grazed shortgrass sites. Brooks (1995), however, found that both diversity and density of small rodents were significantly affected by different grazing treatments. Rosenstock (1996) reported significant differences in species richness and abundance between grazed versus ungrazed sites. Yet, Bich et al. (1995) found that neither diversity nor abundance was affected significantly by heavy grazing in his study, but rather, only proportional species composition. Confounding these contradictions, research on small rodent communities of the Edwards Plateau is extremely limited. A few studies of diversity and habitat use have been conducted recently (Schwertner, 1996; Schwausch, 1997). However, no studies have been undertaken to test specifically for differences in small rodent faunal characteristics on grazed and ungrazed grasslands.

Research on the effects of grazing on grasslands of the Edwards Plateau would be particularly valuable, as overgrazing of rangeland in central Texas is widespread. Overgrazing of this region is a condition that has been further exacerbated by changes brought on by the suppression of wildfire and by urbanization and urban sprawl, which has resulted in habitat loss and habitat fragmentation. Clearly, the impact of heavy grazing on small mammal faunas of shortgrass prairies merits further study.

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