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SMALL MAMMAL COMMUNITIES AND HABITAT ASSOCIATIONS IN THE CHIHUAHUAN DESERT NEAR FORT BLISS, NEW MEXICO

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Desert ecosystems are characterized as some of the most biologically diverse areas in the United States. Many species of flora and fauna are unique to desert habitats. This diversity is in itself phenomenal considering that many species maintain exceptionally stable populations despite unpredictable fluctuations in the environment (Zeng and Brown, 1987). Free-standing water rarely is available in these arid ecosystems. Although the lack of available water would be detrimental for organisms living in most other environments, animals in desert habitats have adaptive morphological and physiological characteristics that enable them to thrive in an environment that is unsuitable for other species (Ghobrial and Nour, 1975). Rodent species with such adaptations especially are diverse in desert ecosystems. Partitioning of resources facilitates coexistence of rodent species in desert rodent communities of southwestern North America; thus desert rodents are ideal subjects for studies of coexistence, competition, and community structure (Heske et al., 1994).

The Chihuahuan Desert is located in the southernmost portion of the Great American Desert and is bounded by the 100th and 108th meridians and the 21st and 33rd parallels (Milstead, 1960). It includes parts of southern New Mexico, all of Texas west of the Pecos River (except for the Guadalupe Mountains), the eastern half of Chihuahua, the western portion of Coahuila, and parts of Durango, Zacatecas, Nuevo Leon, San Luis Potosi, Aguascalientes, and Tamaulipas (Schmidly, 1974). The region has a diverse flora and fauna including eight orders, 24 families, 60 genera, and roughly 119 species of mammals (Schmidly, 1974).

Fort Bliss is an U.S. Army installation in the northern region of the Chihuahuan Desert. It occupies approximately 4,523 km² (452,279 ha), ranging from El Paso County, Texas, to Otero County, New Mexico. This study was conducted on the McGregor Range, which includes the northeastern portion of Fort Bliss. McGregor Range is dominated by desert shrubland, with some desert grasslands, and juniper woodlands

at higher elevations. It is located within the Tularosa Basin, which is typified by lowland valleys, rocky hillsides, and scattered arroyos (Gardner, 1951; Schmidt, 1986; Jorgensen, 1996; Monasmith, 1997). Overall, the region is characterized by a semiarid to arid climate.

Despite studies previously conducted on Fort Bliss concerning the status of small mammals (Jorgensen, 1996; Jorgensen and Demarais, 1996; Root, 1997; Weeks, 1997), few researchers have compared mammalian species across different habitat types. Such a study would provide information about habitat utilization of small mammal species on McGregor Range, thus allowing Fort Bliss personnel to consider these associations when planning military training activities. Such activities have been shown to affect ecosystem stability (Baumgardner, 1990; Brattstrom and Bondello, 1983; Carroll et al., 1999; Edwards et al., 1998; Gese et al., 1989; Shaw and Diersing, 1990; and Stephenson et al., 1996) and therefore should be considered when planning military operations.

Due to the steady increase in human population and urbanization of surrounding public lands, it is be-

coming necessary for military personnel to ecologically manage the acres of non-developed land on their properties in order to preserve areas for existing wildlife and to assure sound stewardship of public lands. Information provided by this project will be used to better understand and manage these biological resources, and minimize the potential impacts of military training in these environments. For example, such information could be used to avoid areas of high rodent diversity and density, as well as to identify habitats with unique rodent compositions.

The objectives of this study were to: (1) compare small mammal composition (rodents) among 12 unique habitats on McGregor Range to determine if certain habitats support rodent communities of higher diversity, (2) compare small mammal densities per habitat and determine any influence of vegetative cover, (3) determine if the amount of rainfall influences density or diversity, (4) determine the survivability of each species, and (5) compare the average activity among species and habitats to determine the influence of vegetative density on rodent activities.

METHODS

The research design for this study involved sampling small mammals in 12 distinct habitats. Range botanists from Fort Bliss characterized each habitat based on vegetative composition and density, and labeled them as sandy arroyo scrub, nonstabilized dune, coppice dune, creosote-tarbrush scrub, mixed desert scrub, grama grassland, creosote grassland, yucca grassland, swale, acacia hillside, *Chilopsis* (desert willow) arroyo, and succulent hillside habitats. Each habitat type was ranked by range botanists on the basis of percent vegetative cover from 1 (0.0-20.0%) to 5 (80.0-100.0%). The experimental design for this project was described in Clary et al. (1999). Two grids, each with census and assessment lines, were constructed for each habitat. Census lines, consisting of two parallel trap lines 30 m apart (240 m in length) with trap stations placed at 10 m intervals along each line for a total of 50 traps were used for initial captures. The assessment lines, containing 72 traps, formed a diamond-like configuration about the census lines and were

utilized for recording recaptures on each grid. Each of these lines (census and assessment) was sampled using Sherman live-traps (H. B. Sherman Trap Co., Tallahassee, FL) baited with birdseed and rolled oats during two seasonal periods (Spring and Fall) for two consecutive years (1997 and 1998). Typically, sampling of the grids occurred on three consecutive nights on the census lines followed by sampling for an additional three consecutive nights on the assessment lines, for a total of 35,136 trap nights. We recorded Texas Tech Museum identification number, species, weight, sex, toe-clip number, trap station, and date of capture for each individual captured on the census line. All individuals were released at the site of capture. Captures on assessment lines were identified from toe-clip patterns and the date and trap station of capture was recorded. For this study, it was assumed that animals encountered traps randomly in a particular habitat and neither sex, age, or dominance of an individual influenced capture probabilities.

A reference collection of voucher specimens and tissue samples of at least one adult male and one adult female of each species was prepared and deposited in the Museum, Texas Tech University. In addition, toes obtained during the toe-clipping procedures were preserved in lysis buffer (Longmire et al., 1997) and serve as voucher material. Nomenclature followed Jones et al. (1997) and specimens were identified using keys and characteristics from Davis and Schmidly (1994), Findley (1987), and Findley and Caire (1974).

To determine monthly precipitation, a rain gauge was attached to a T-post and placed at the first trap station of each grid. Mineral oil was added to the gauges to prevent evaporation. Rainfall was recorded (in millimeters) at the first of each month from April 1997 to October 1998. The pattern of rainfall for each month was recorded for each habitat and season. In some cases, minor disturbances on the grids (e.g., cattle) affected the reliability of some of the gauges and monthly accumulation could not be recorded. These incidences were not included in the accumulation averages of the affected grid.

All statistical analyses used in this study were generated in the software program Matlab (Matlab 5.2, 1998; www.biol.ttu.edu/faculty/facpages/strauss/matlab.htm). Species diversity was calculated for each grid and habitat using Simpson's diversity index D_s (Simpson, 1949). Species diversity values were compared between and among habitats to determine which habitats possessed the highest diversity. Diversity values were compared to the vegetative density (percent cover) of each habitat using correlation analyses. Species composition was compared among the habitats by grouping habitats via a UPGMA cluster analysis of species frequencies for each habitat. The cluster analysis was bootstrapped for 1,000 iterations and those habitats grouping together at least 50% of the time (bootstrap support value = 0.50) were recognized. Clustering methods similar to those used by Brown and Heske (1990) were used to determine species composition similarities among the habitats. The average

rainfall from each trapping period was tabulated and compared with each habitat's diversity value through correlation analyses to examine the relationship between rainfall and rodent community diversity.

Rodent density per habitat, estimated as the number of individuals for all species captured per hectare, was compared among habitats and seasons. Percent cover (vegetation) per habitat also was compared with rodent density. In addition, regression analyses were used to examine the relationship between rainfall and density.

Survivorship was estimated for each species and comparisons were made using the proportion of individuals (per species) recaptured from the total initial captures at six-month intervals (6, 12, and 18 months). In addition, survivorship rates were estimated by log-log regression of number of recaptures since first capture. It should be noted that this estimate does not distinguish between death and emigration.

The average activity of individuals per species was estimated by converting the trap stations and traps of capture per grid to points on an x,y point-coordinate system. The centroid (median) of activity for each recaptured individual was generated based on the assemblage of captures and deviations from the centroid to each trap of capture were calculated. The squared deviations were then averaged per species (mean squared deviations, MSD) and compared among the species. In addition, the squared deviations were compared across habitats to determine whether differences in vegetative density (percent cover) among the habitats affected the amount of activity among the residing species. An analysis of variance (ANOVA) was used to determine significant differences among the species and habitat activity averages. Post-hoc multiple comparisons based on sequential Bonferroni probabilities (Rice, 1989) were used to determine significant pairwise differences within the species and habitat groups.

RESULTS

Diversity.—Nineteen species were captured from the 12 habitats. The sandy arroyo scrub habitat possessed the highest rodent diversity ($D_s = 0.872$), although several other habitats possessed similar diversity values, including *Chilopsis arroyo* (0.828), *Acacia hillside* (0.816), creosote-tarbush scrub (0.816), succulent hillside (0.803), swale (0.802), *Yucca grassland* (0.796), creosote grassland (0.742), and mixed desert scrub (0.707) habitats (Table 1). Species diversity was lowest in the coppice dune habitat (0.384), whereas nonstabilized dunes (0.645) and grama grasslands (0.472) had low to medium diversity values. Species diversity in the habitats was positively correlated ($r = 0.74$, $p < 0.001$) with percent vegetative cover.

Species diversity for most grids remained relatively unchanged between trapping periods (Spring 1997, Fall 1997, Spring 1998, and Fall 1998) and between years (1997, 1998). However, small mammal diversity increased in the nonstabilized dune habitat during 1998 (Spring and Fall), decreased in the coppice dune habitat during 1998 (Spring and Fall), decreased in the mixed desert scrub habitat during Spring 1998, and was lowest in the yucca grassland habitat during Spring 1997.

All interpretations on community diversity as a function of rainfall were based on direct observation and correlation analyses (Figure 1). Average rainfall in Spring 1998 was the lowest (5 mm) recorded during

Table 1. The Simpson's diversity index D_s (Simpson, 1949), used to estimate species diversity per season for each of the 12 habitats on Fort Bliss Military Base. Total diversity values for each habitat for all four seasons are provided in the last column.

Habitat	Spring 1997	Fall 1997	Spring 1998	Fall 1998	Total
Nonstabilized Dune	0.552	0.541	0.735	0.696	0.645
Sandy Arroyo Scrub	0.876	0.881	0.865	0.807	0.872
Mixed Desert Scrub	0.738	0.779	0.480	0.607	0.707
Swale	0.772	0.768	0.891	0.799	0.802
Succulent Hillside	0.788	0.804	0.690	0.766	0.803
<i>Chilopsis</i> Arroyo	0.865	0.823	0.776	0.749	0.828
<i>Acacia</i> Hillside	0.831	0.858	0.802	0.821	0.816
Grama Grassland	0.393	0.452	0.521	0.540	0.472
Creosote Grassland	0.747	0.663	0.813	0.745	0.742
Creosote-Tarbush Scrub	0.835	0.793	0.755	0.754	0.816
Coppice Dune	0.423	0.532	0.228	0.244	0.384
<i>Yucca</i> Grassland	0.599	0.870	0.818	0.708	0.796

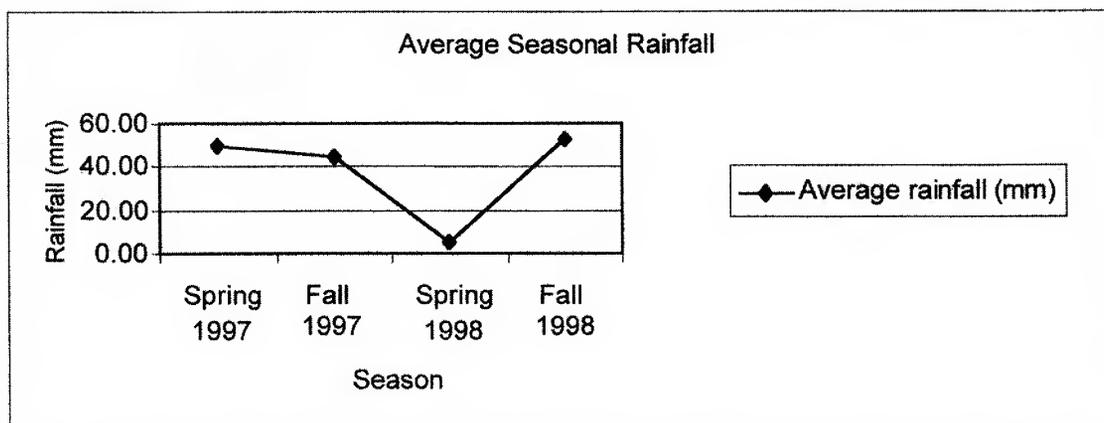
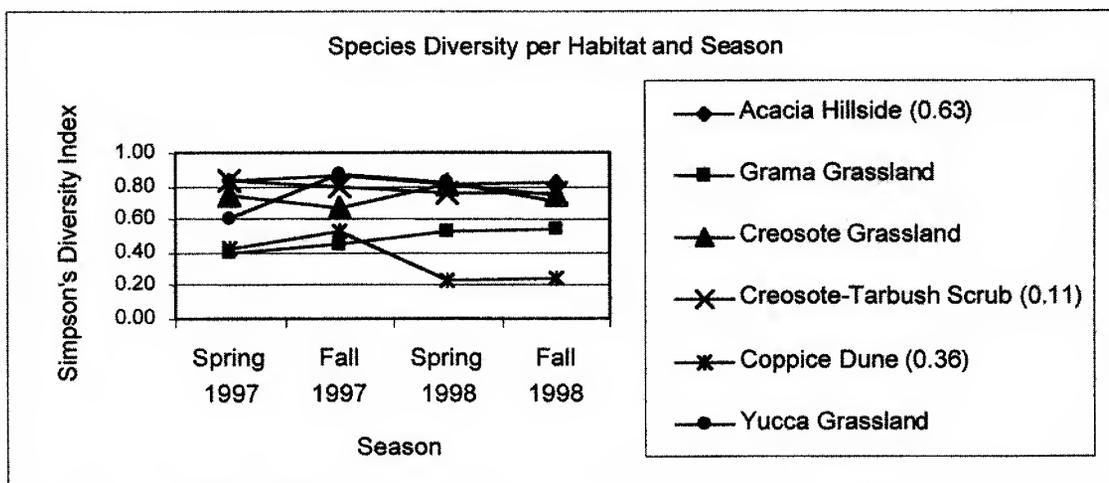
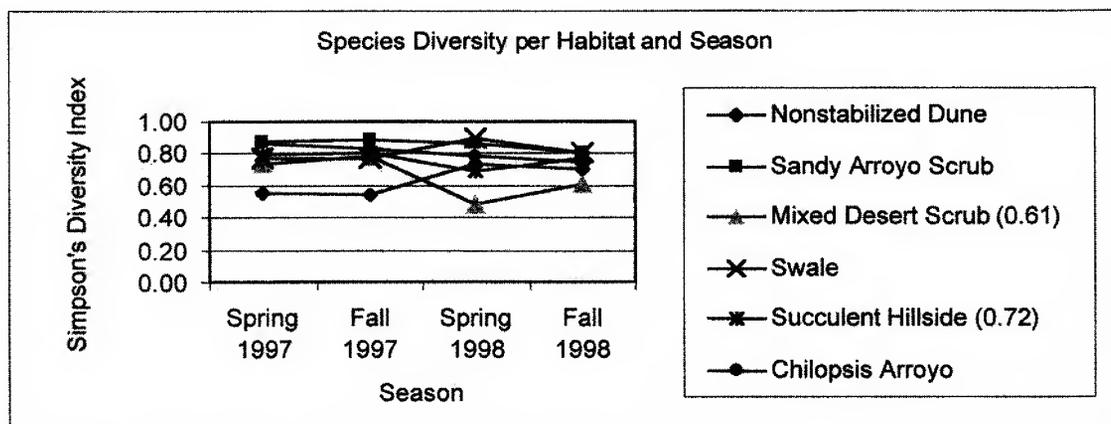


Figure 1. Species diversity values per habitat and season compared with season rainfall averages. Positive coefficients are shown in parentheses.

the study; whereas Spring 1997, Fall 1997, and Fall 1998 averaged approximately 50 mm of rainfall similar. Seasonal diversity values were positively correlated with seasonal rainfall in the mixed desert scrub ($r = 0.76$, $p = 0.23$), succulent hillside ($r = 0.90$, $p = 0.10$), Acacia hillside ($r = 0.64$, $p = 0.35$), creosote-tarbrush scrub ($r = 0.46$, $p = 0.53$), and coppice dune ($r = 0.47$, $p = 0.53$) habitats. However, none of these positive correlations were significant ($p > 0.05$).

The UPGMA cluster analysis revealed certain habitats grouping together by species composition similarities, with bootstrap support values of at least 0.50 (Figure 2). The coppice dune and mixed desert scrub habitats clustered with a bootstrap support value of 0.55 and the three grasslands (creosote grassland, grama grassland, and Yucca grassland) clustered with a bootstrap value of 0.58. In addition, the acacia hillside, sandy arroyo scrub, and succulent hillside habitats clustered with a bootstrap support value of 0.71 with two of the habitats, acacia hillside and sandy arroyo scrub, clustering with a bootstrap support value of 0.85.

Density.—Rodent densities were estimated within habitat by calculating the number of captured individuals per hectare (Figure 3). The swale habitat exhibited the highest rodent density of 39.2 individuals/ha (Figure 3). Other habitats having relatively high rodent densities were the Acacia hillside (38.8 individuals/ha), *Chilopsis* arroyo (33.4 individuals/ha), and creosote grassland (30.0 individuals/ha) habitats. The lowest rodent density (10.0 individuals/ha) was found in the coppice dune habitat. The grama and Yucca grassland habitats also contained relatively low rodent densities (17.9 and 21.3 individuals/ha, respectively).

Relationships between vegetation and rodent densities for each habitat were examined by correlation analyses. Percent cover of vegetation and rodent density were positively, but not significantly correlated across all habitats ($r = 0.65$, $p > 0.05$). In addition, regression analyses were used to estimate the influence of rainfall accumulation on rodent densities per season. Although there appeared to be a decrease in density within some of the habitats during low accumulation periods, none of the regressions were significant.

Survivorship.—The proportion of individuals recaptured from the total number of initial captures was calculated at six-month intervals for each species (Figure 4). Individuals of 16 species captured in the initial census were recaptured after six months (Figure 4). Due to deficient sample sizes, *Spermophilus spilosoma*, *Perognathus flavescens*, *Chaetodipus hispidus*, and *Reithrodontomys montanus* were excluded from the regression analysis. The percentage of recaptures per species ranged from 3.3% for *Neotoma micropus* to 26.1% for *Dipodomys merriami*. Individuals of 13 species were recaptured at 12 months, with the recapture rates per species ranging from 0.7% for *Sigmodon hispidus* to 11.1% for *Dipodomys spectabilis*. Six of the 13 species were from the family Heteromyidae and possessed the highest recapture rates (3.4–11.1%). Individuals of 10 species were recaptured after 18 months with six of the species from the family Heteromyidae. Recapture rates ranged from 0.7% for *Peromyscus leucopus* and *Peromyscus maniculatus* to 11.1% for *D. spectabilis*.

Results from the regression analysis indicated *N. micropus* had the highest exponential rate of decline ($d = -0.56$) from the beginning to the completion of the study. Other species with high exponential rates of decline were *Onychomys arenicola* ($d = -0.39$), *S. hispidus* ($d = -0.37$), and *Reithrodontomys megalotis* ($d = -0.35$). *D. merriami* had the lowest exponential rate of decline ($d = -0.18$) followed by *Chaetodipus intermedius* ($d = -0.185$), *Dipodomys ordii* ($d = -0.19$), *Perognathus flavus* ($d = -0.21$), and *Chaetodipus eremicus* ($d = -0.21$).

Activity.—When calculating the average activities by individuals of each species, six were eliminated on the basis of inadequate sample size: *P. flavescens*, *C. hispidus*, *D. spectabilis*, *R. montanus*, *N. micropus*, and *S. spilosoma*. The MSD were calculated from the centroid (spatial mean of activity to each trap station of capture) and averaged for each species per habitat type (Figure 5). The averages among the remaining 13 species differed significantly ($F = 3.65$, $df = 18$, $p < 0.001$). *Onychomys leucogaster* had the widest activity range (3.94 MSD) followed by *P. maniculatus* (3.87 MSD), *D. merriami* (3.81 MSD), *O. arenicola* (3.72 MSD), and *D. ordii* (3.71 MSD). The lowest average activity range of 2.50 MSD was exhibited by

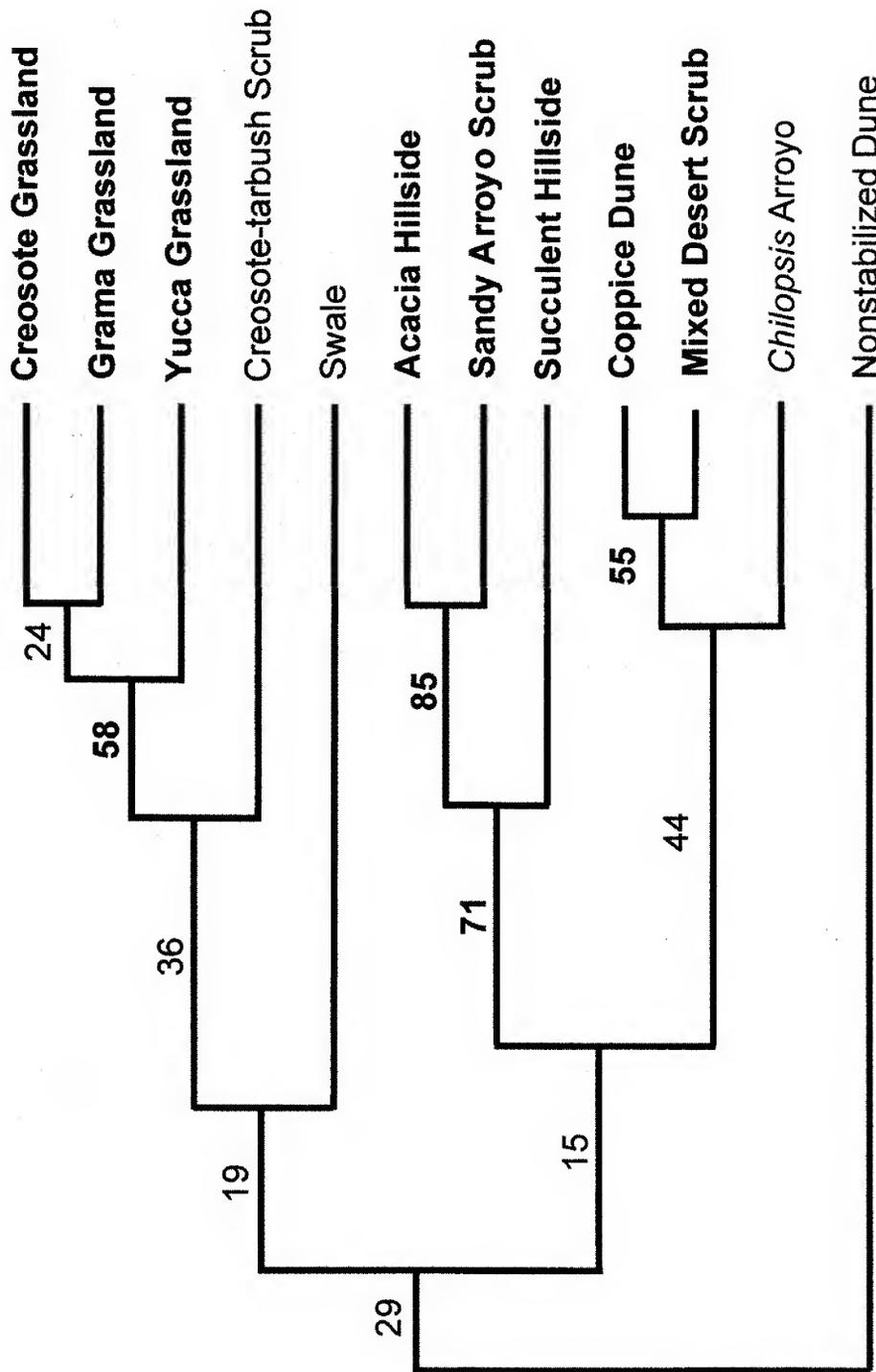


Figure 2. A cluster analysis depicting habitats that grouped together based on similarities of rodent species composition. Clusters with a bootstrap support value of $\geq 50\%$ are shown in bold.

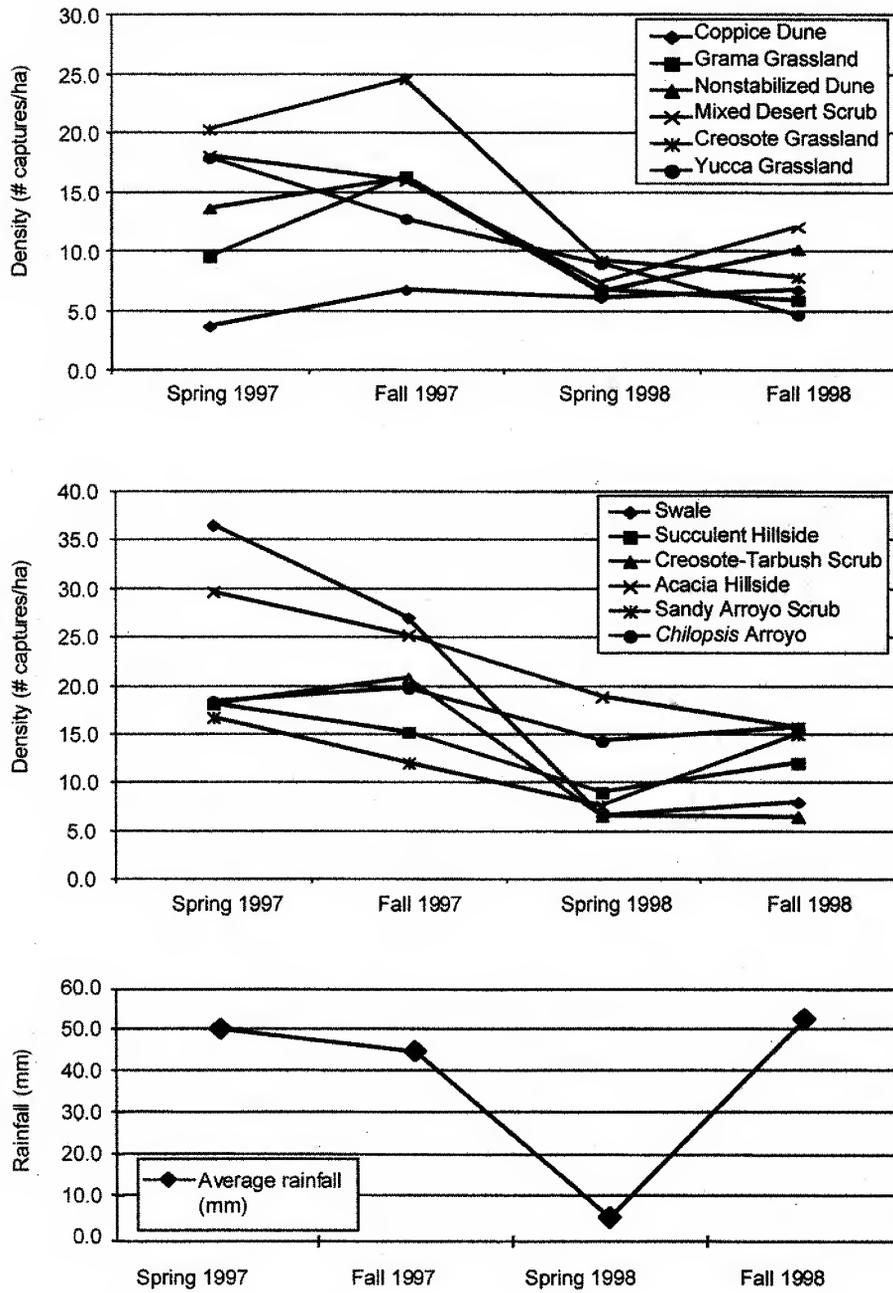


Figure 3. Rodent density, defined as the number of captures per hectare, for each of the four trapping periods at Fort Bliss.

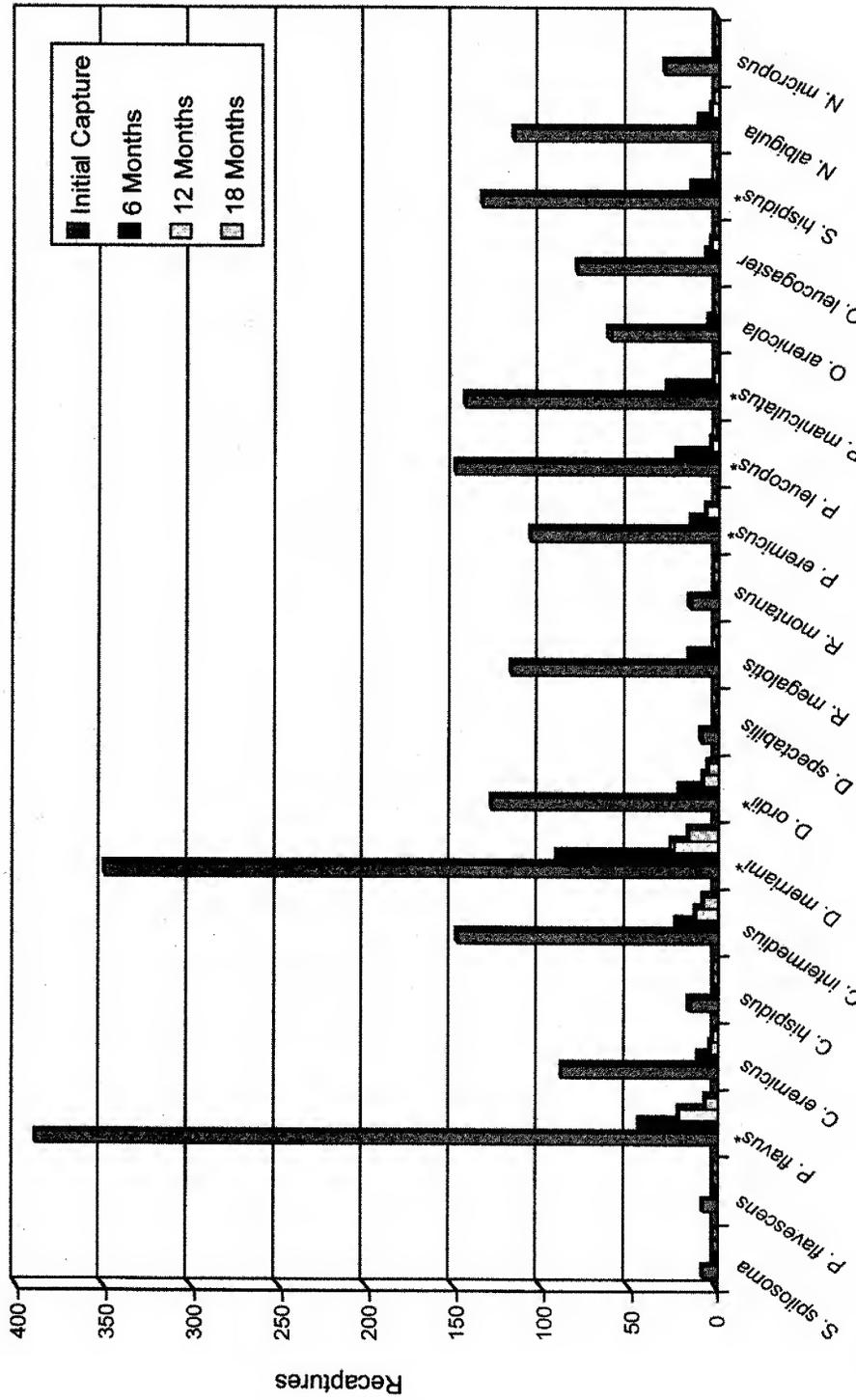


Figure 4. Survivorship for each species based on percentages of recaptures taken from the total initial captures at 6, 12, and 18 months. An “*” indicates species having a significant value ($p < 0.05$).

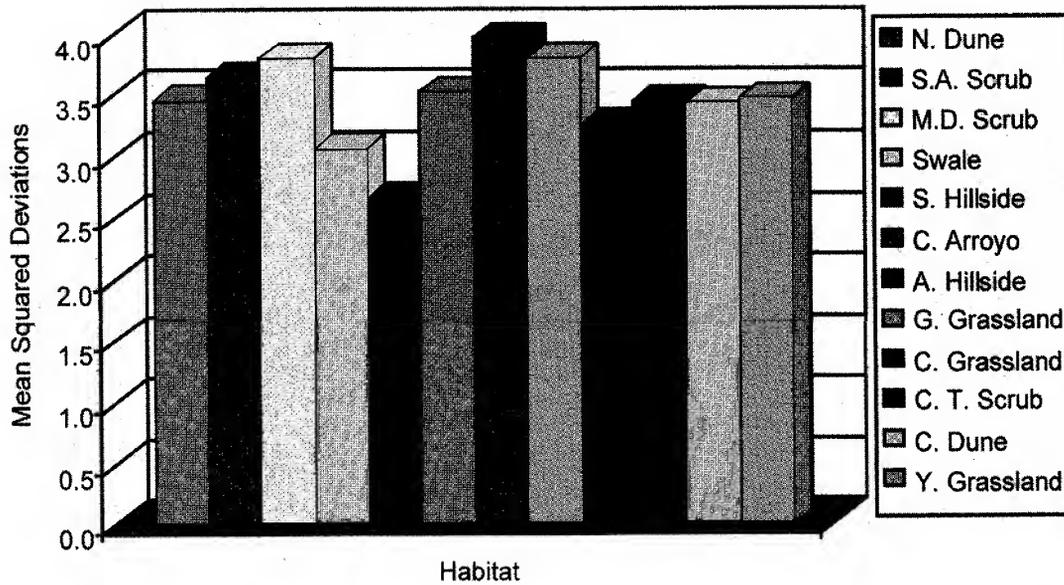
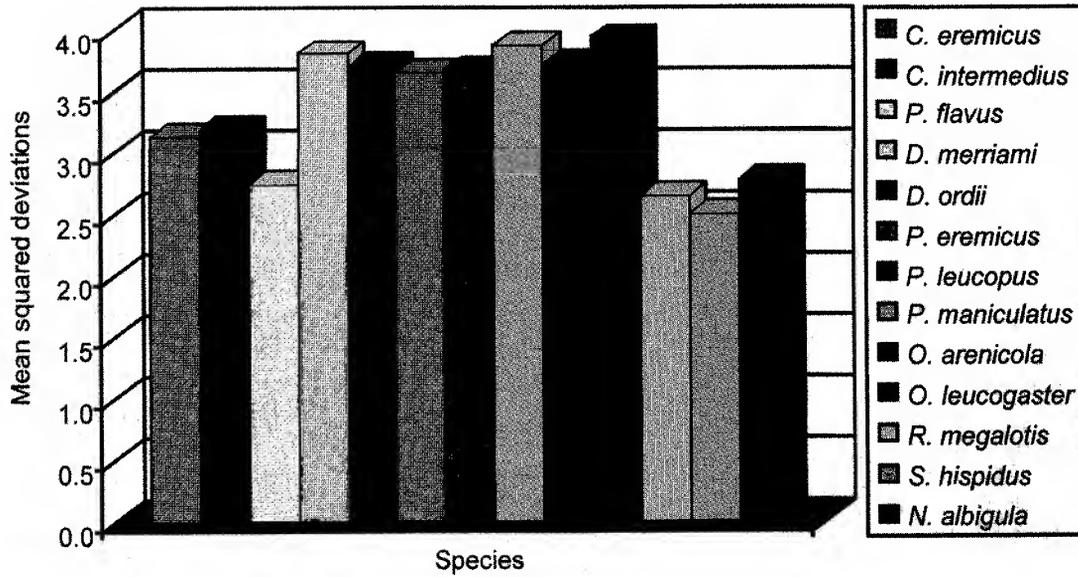


Figure 5. Average species movements shown as the mean squared deviation from the centroid activity for each species (top) and habitats (bottom). An analysis of variance detected significant differences for species ($p < 0.00$) and for habitats ($p = 0.002$).

S. hispidus. Other low values were found for *R. megalotis* and *P. flavus* with averages of 2.65 and 2.74 MSD, respectively.

The averaged MSD across species also was compared among the 12 habitats (Figure 5). Values differed significantly (2.68, 11, $p = 0.002$) with the highest recorded for small mammals from the acacia hillside habitat (3.96 MSD). Similar results were found

for rodents from the grama grassland and mixed desert scrub habitats with 3.80 and 3.79 MSD, respectively. Results indicated that the lowest average activity value was for small mammals from the succulent hillside habitat with 2.66 MSD. Results were similar in the swale and creosote grassland habitats (3.06 and 3.26 MSD, respectively). Despite the significant differences found from the ANOVA generated across species and habitat groups, no significant differences resulted in the pairwise comparisons within each group.

DISCUSSION

With few exceptions, there appeared to be little difference among diversity values in reference to trapping period or year within the same habitat type. This may be expected due to the short duration of the study and overall lack of long-term data for this environment. The low diversity seen in coppice dune habitats (which contained mainly *D. merriami* and *D. ordii*) was possibly a result of kangaroo rats being more efficient or successful foragers in open habitats when compared to other species. Overall, these findings are similar to those of Harris (1984), Kotler (1984), and Kotler and Brown (1988). Unfortunately, with the exception of Jorgensen (1996) few comparative studies are available for Chihuahuan Desert communities.

In terms of overall species diversity, habitats characterized by high percent vegetative cover (> 60%) including the swale, *Chilopsis* arroyo, sandy arroyo scrub, and Acacia hillside habitats possessed the highest species diversity. Brown (1975) suggested that habitats with higher productivity show less competition among species. Conversely, the coppice dune habitat (< 20% vegetative cover) consistently demonstrated a paucity of small mammals. There is little cover and fewer seed-producing plants associated with this habitat, and seed production is the key determinant of rodent species diversity in North American desert ecosystems (Brown, 1975). Diverse communities of small mammals have been found to exist more frequently in densely vegetated habitats than in sparsely vegetated habitats (Jorgensen, 1996; Brown and Zeng, 1989). In a study of desert rodent communities in the Mojave Desert, species diversity increased with increasing vegetative cover (Hafner, 1977). However, in our study we did not examine seed production, there-

fore we could not discern between the effects of vegetative cover in terms of protection from predators or as a means of food production. Also, seed size and utilization by small mammals may effect species distribution and density.

Although the results in the correlation analyses were not significant, the decrease in rodent diversity observed in some of the habitats during Spring 1998 may be due to the low average precipitation recorded within that season. Fluctuations in rainfall directly affect water and forage availability. Water accessibility may play a significant role in coexistence of desert rodents. The effects of available moisture, vegetative density, and habitat complexity are intricately involved in determining the diversity of rodent communities (Christian, 1980; Hafner, 1977).

In addition to exhibiting high rodent diversity, habitats characterized by dense vegetation (> 60% vegetative cover) also contained higher densities of rodents. The swale habitat had the highest percent vegetative cover (80-100%) and also exhibited the highest rodent density. Although not significant, results from the correlation analyses revealed a positive correlation between rodent density and percent cover of vegetation. High densities of rodents in densely vegetated habitats may be due to an increase in forage (seed-producing plants, vegetation, or insects). As noted by Thompson (1982), the mean densities of seeds and the variation in those densities are greater beneath vegetation. In addition, the ample amount of vegetation may be beneficial as adequate cover to serve as protection from predators (Kotler and Brown, 1988).

A positive correlation was revealed between seasonal rodent density and rainfall. The drought period in Spring 1998 seemed to have an adverse effect on rodent density in most of the habitats. For example, the mixed desert shrub and creosote-tarbrush scrub habitats showed a decline in total number of species present during Spring 1998. Eleven species present during 1997 were absent from these habitats in Spring 1998, most notably absent were *O. leucogaster*, *O. arenicola*, *P. eremicus*, *P. leucopus*, *P. maniculatus*, and *S. hispidus*. As discussed above, water availability is crucial to most rodent species. Although heteromyids do not drink water, times of low resource availability resulting from low rainfall can cause a slower rate of reproduction for some species.

Only 2.0 % of the total number of individuals captured across species were recaptured after 18 months. The probability of survival may vary with individual characteristics and also as a function of various environmental variables (Lebreton et al., 1992). For example, six out of the 10 species of the family Heteromyidae had individuals recaptured after 18 months (ranging from 1.6% to 11.1% of initial captures). Their success may be due to certain morphological and metabolic adaptations characteristic of this family. For example, individuals of the genus *Dipodomys* have many attributes, such as inflated auditory bullae and bipedality, which enhance senses and speed for avoidance of predators in addition to foraging efficiency. Other members of the family Heteromyidae, including *Chaetodipus* sp. and *Perognathus* sp., are known to aestivate during times of low seed availability. Interestingly, species of *Neotoma* were seldom recaptured. It is unclear if woodrats became trap-shy (due to their large size) or whether their survival rates were low.

Higher averages of activity were present in the habitats characterized by relatively sparse vegetative cover (< 40% cover). These sites were primarily domi-

nated by bipedal species (*Dipodomys* sp.), while more densely vegetated sites (> 40.0% cover) contained primarily quadrepedal species. Some microhabitat theories suggest that morphological adaptations associated with locomotion allow individuals to utilize specific microhabitats (Price, 1978; Price and Brown, 1983; Kotler, 1984). Large, bipedal kangaroo rats (*Dipodomys* sp.) are associated with open microhabitats, while small, quadrepedal pocket mice (*Perognathus* sp.) are associated with shrubby microhabitat (Harris, 1984; Root 1997). For *D. merriami*, the presence of open areas is the most important factor affecting its distribution (Congdon, 1974). Alternatively, more dense habitats such as swales and sandy arroyo scrub may be critical in maintaining populations of *N. micropus*, *P. leucopus*, and *S. hispidus*.

The high average activities in *Onychomys* sp. may be the result of their feeding guild (carnivorous). Having a diet consisting of primarily insects may require members of this genus to travel greater lengths in pursuit of food in comparison to coexisting herbivores. The low average activity found in *S. hispidus* may be a result of its herbivore characteristics as well. This herbivorous species predominately was found within the swale habitat, which contained the lowest average activity across species and is characterized by abundant, dense vegetation (> 80% vegetative cover).

Stable population dynamics cannot be attributed to any single combination of traits (Brown and Zeng, 1989). Likewise, variation in species diversity, rodent density, and survivorship cannot be attributed to a single environmental factor. Vegetative composition and density as well as rainfall have been shown to be factors affecting rodent community ecology. Not surprisingly, ecological components of the desert ecosystem are intertwined, and the organization of a community and its patterns of temporal change reflect the fluctuations of species populations that comprise the community (Brown and Heske, 1990).

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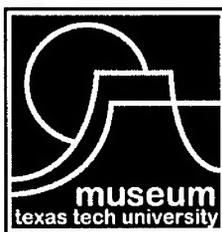
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It was through the efforts of Horn Professor J Knox Jones, as director of Academic Publications, that Texas Tech University initiated several publications series including the Occasional Papers of the Museum. This and future editions in the series are a memorial to his dedication to excellence in academic publications. Professor Jones enjoyed editing scientific publications and served the scientific community as an editor for the Journal of Mammalogy, Evolution, The Texas Journal of Science, Occasional Papers of the Museum, and Special Publications of the Museum. It is with special fondness that we remember Dr. J Knox Jones.

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