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Numerous studies have been made of rodent population and community dynamics, especially in arid ecosystems. Most have centered on understanding how total and species-specific densities of rodents change over time. The standing biomass each species contributes also is important to the energy available to the mesocarnivore community. Although density and standing biomass are related, how they might differ and if those differences are of importance to community structure and function have not received much attention. We analyzed 12 years of rodent density and body mass data from the Chihuahuan Desert in northern Mexico. Data were collected yearly in spring and fall from radial livetrapping webs. Total density and biomass changed significantly in a parallel manner from year to year, and both were related to precipitation and percent cover of grass and forbs. Based on density and biomass, the rodent community was dominated by 2 or 3 principal species. However, on a species-specific level, the numerically dominant species was a small-bodied granivore (*Chaetodipus nelsoni*), and a large-bodied folivore (*Neotoma albigula*) dominated in biomass. As total density increased, the proportion contributed by dominant species decreased. As total biomass increased, the proportion in the 2 dominant species increased and accounted for approximately 80% of total biomass. Over the 12 years of the study, species distributions based on density showed no directional change. In contrast, biomass of the rodent community gradually concentrated in a single, large-bodied folivore, *N. albigula*. Although total density and biomass responded similarly to precipitation and plant productivity, considerable differences between these 2 characteristics existed in their species-specific contributions to and changes within the community. The significance of these differences relative to foraging strategies and variable feeding opportunities within the community is discussed.

Key words: biomass, Chihuahuan Desert, density, rodent community

Numerous studies have been made of rodent population and community dynamics, especially in arid ecosystems (Brown and Ernest 2002; Brown et al. 2001; Brown and Heske 1990; Ernest 2005; Ernest et al. 2000; Hernández et al. 2005; Lima et al. 2008; Meserve et al. 2003; Previtali et al. 2009; Thibault et al. 2004; White et al. 2004). Most of these studies have centered on understanding how total and species-specific density of rodents change over time and how bottom-up factors such as precipitation and top-down factors such as predation and competition influence these changes (Brown and Ernest 2002; Ernest et al. 2000; Hernández et al. 2005; Meserve et al. 2003; Previtali et al. 2009; Wang et al. 2001). Although these studies of density or abundance or both have provided extensive information about population and community dynamics, analyzing density alone has not been sufficient to explain changes in community dynamics.

One of the fundamental ecological roles of the rodent community, especially in desert environments, is providing standing biomass for secondary consumers (Hernández et al. 2002; Laundré et al. 2009). Although total standing biomass generally parallels total density of rodents, they occasionally diverge (Ernest 2005; Thibault et al. 2004; White et al. 2004). Because the amount of biomass in the rodent community is the sum of species-specific contributions in density multiplied by their body mass, any change in species density ratios—for example, greater increases in density of small-bodied species versus large-bodied ones (White et al. 2004)—will decouple the total community density–biomass relationship. In these

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cases changes in total density do not reflect changes in total biomass available. Also, because of differences in body mass, the densities of each species often do not parallel their specific biomass contributions to the community; for example, *Chaetodipus* sp. can be a numerically dominant species (Hernández et al. 2005), but at 13–14 g it might contribute little to the overall biomass of the community. This underscores the importance of knowing species-specific contributions to total biomass of the rodent community.

Because of foraging preferences of predators, the amount and distribution of biomass among the species of rodents can have differential impacts on the carnivores within a system. For example, biomass of nocturnal kangaroo rats (*Dipodomys* spp.) benefits owls but only occasionally diurnal hawks. Because of these foraging preferences in carnivores, temporal changes in the amount and distribution of biomass among rodent species can have profound effects on the secondary consumer community. Numerical increases in *Chaetodipus* spp. not only would result in minor increases in community biomass but also contribute little to rodent biomass available to coyotes (*Canis latrans*), which rarely prey on these species (Hernández et al. 2002). Thus, it is important to understand how densities of rodent species change over time and what corresponding changes occur in biomass amounts and distribution among species.

Few studies of density of rodents in arid environments have considered corresponding biomass amounts and distribution and how they change over time. Ernest (2005) demonstrated that body size-energy distributions (= biomass$^{3/4}$) differed among rodent communities across several arid sites. She also found that in most cases the BSED did not correspond to relative densities; for example, although large-bodied species were less abundant, because of their larger body size, they contributed more to body size-energy distributions than indicated by their relative density. In a northern Chihuahuan Desert site biomass amounts changed over time and often, but not always, paralleled density changes (Ernest and Brown 2001; Thibault et al. 2004; White et al. 2004). These changes in biomass also were accompanied by shifts in biomass distribution among species, specifically with increases in smaller-bodied species (*Chaetodipus baileyi* and *C. penicillatus*) over time.

The results of these studies indicate that the density of individual species does not necessarily reflect its contribution to overall community biomass. Also, as rodent density varies over time, underlying shifts in the amount and species-specific distribution of biomass can occur within the community. However, because most of the analyses were not species-specific, the details and implications of these shifts are not well understood. Additionally, because of study objectives, existing studies often were limited to just the granivore portion of the rodent community. Some of the major contributors to community biomass can be large-bodied folivores (e.g., *Neotoma* spp.) and omnivores (e.g., *Spermophilus* spp.). Both of these groups also can be important food sources for predators (Giovanni et al. 2007; Hernández et al. 2005; Laundré et al. 2009); thus, their contributions to density and biomass need to be investigated in detail.

Extensive analyses exist regarding impacts of bottom-up factors such as precipitation and plant productivity on species density and diversity (Brown and Ernest 2002; Ernest et al. 2000; Hernández et al. 2005; Meserve et al. 2003; Previtali et al. 2009; Wang et al. 2001). However, few parallel analyses have been made regarding the role of these factors in changes to biomass amounts and distribution within rodent communities. White et al. (2004) attributed the shift in species-specific biomass they noted to possible habitat changes but did not present a specific analysis of the effects of climate. If such shifts are related to habitat changes, this underscores the importance of variation in foraging strategies based on habitat makeup and resulting predation risk to bottom-up processes (Brown 1989a, 1989b; Brown et al. 1994; Kotler et al. 1993). Because of foraging specificity between and even within different foraging groups—for example, granivores and folivores—changes in species-specific biomass and density can relate to shifts in the specific types of food available—for example, seeds versus plant tissue—or the conditions for obtaining these resources. However, it is unclear as to whether such factors impact biomass amount and its species-specific distribution in a manner similar to how density is affected.

A comparative study is needed on how species-specific contributions to density and biomass amounts are distributed within the rodent community, how they change over time, and how bottom-up forces might affect those changes. Such an analysis could provide insights into relationships between density and biomass within the rodent community and if bottom-up factors such as precipitation and plant productivity affect density and biomass differently. Documenting these changes also might show how the impact of bottom-up forces can be influenced by different foraging strategies among species. Details of these relationships can be helpful in understanding how availability of rodent community biomass affects secondary consumers.

To provide this species-specific comparative analysis within the complete rodent community (granivores, folivores, and omnivores), we used a 12-year data set on rodent density and biomass in the Chihuahuan Desert in Mexico. Based on previous study results (Ernest 2005; White et al. 2004), our working hypothesis was that density and biomass would be positively related. Resulting predictions we tested were that species-specific and functional group (granivores, folivores, and omnivores) contributions to total density will not differ from their contributions to total biomass, that annual species-specific variations in their contributions to total density and biomass will not differ, and that precipitation and plant productivity levels affected total density and biomass production and distribution in a similar manner.

Materials and Methods

We conducted the study from 1996 to 2007 in the Mapimí Biosphere Reserve in the Chihuahuan Desert of northern Mexico (26°40′N, 103°40′W). The average mean temperature of the coldest month (January) was 11.8°C. The highest average summer temperature (28°C) occurred in June (Cornet 1988). The 28-year average January–December rainfall was 280.4 ± 19.4 (*SE*) mm

with a large amount of year-to-year variation (range = 122–510 mm). Approximately 78% of the total yearly rainfall amount is in the rainy season from June to September (Cornet 1988).

Our field efforts were in 2 distinct habitat types, a grassland dominated by tobosa grass (*Pleuraphis mutica*) and a shrubland dominated by mesquite (*Prosopis glandulosa*), creosotebush (*Larrea tridentata*), and prickly pear cacti (*Opuntia rastrera*). We trapped twice per year (seasonal treatment)—spring (March) and fall (November)—over the 12 study years (annual treatment). We considered the fall sample as an estimate of density after the reproductive season and the spring sample a representation of the population size in advance of the next breeding season. Because the normal January–December year does not correspond to biologically significant events, annual or 12-month precipitation amounts were obtained by summing monthly precipitation amounts from the 12 months prior to the sample dates. For the fall sample dates this period was from November of the previous year to October just before the sample date. For the spring sample it was from March of the previous year to February.

We used percent plant cover as a relative measure of plant productivity (Ernest et al. 2000; Flombaum and Sala 2007). To estimate plant cover we established 4 randomly placed 36 × 36-m quadrats in each of the 2 study habitats. Each quadrat had 36 (6 × 6) sample points spaced 6 m apart. At each point we measured percent cover of shrubs, cacti, forbs, and grasses within a 1 × 1-m point intercept frame (Floyd and Anderson 1982). Vegetation measurements were made in November and March of each year. We limited our analysis to percent cover of forbs and grasses because they are the primary food sources of most rodents (Murray and Dickman 1994; Reichman 1975).

To estimate the density and biomass of the rodent community in the grassland and shrubland areas we used 3 radial trapping grids or webs (treatment replicates—Parmenter et al. 2003) per vegetation community (habitat treatment; grassland and shrubland). In each web we placed 145 Sherman traps (7.6 × 8.9 × 30.5 cm; H. B. Sherman Traps, Inc. Tallahassee, Florida) in twelve 100-m lines, each radiating from a central point. We placed 12 traps along each line, the first 4 at 5-m intervals and the remainder at 10-m intervals, plus 1 in the center. With the inclusion of a 5-m peripheral buffer, each web was 3.4 ha in area. We trapped 3 nights per season, checking and rebaiting traps in the morning (0600–0700 h) and afternoon (1700–1800 h). For the 1st capture of all rodents we recorded the species and body mass of each individual. We marked these individuals with a marking pen and released them. Although the Instituto de Ecologia, A.C., does not have an animal care and use committee, our handling procedures were consistent with guidelines of the American Society of Mammalogist for use of mammals in research (Gannon et al. 2007). We used the total number of 1st captures per web area to estimate density per web of each species. Biomass per web of each species was estimated by adding up individual body mass of 1st-caught individuals.

We used a 3-way analysis of variance (ANOVA) design to test the null hypothesis that rodent densities, or biomasses, were equal in both habitats, over the years, and in both seasons. Data met the assumptions of normality and homoscedasticity. To test for relationships between density or biomass with precipitation and productivity, we initially used a multiple linear regression model with precipitation and percent forb and grass cover as the 3 independent variables. However, we found that these variables were highly correlated and because of this colinearity, we chose to use simple linear models to analyze their individual potential relationship with rodent density and biomass. The dependent variable was either density or biomass per hectare, and we 1st used the amount of precipitation received or productivity estimates of the previous year and subsequently the amount received 2 years prior to that as the independent variables. Similar to Ernest et al. (2000), we did not use a Bonferroni correction for repeated regressions because we were investigating patterns of variation between density and biomass and not whether specific relationships were significant.

We conducted the ANOVA and all regression analyses with Sigmastat version 3.5 software (Systat Software, Inc., Point Richmond, California). We used the $P \leq 0.05$ rejection level for all statistical tests. All r^2 values are adjusted for sample size, and means are presented with *SE*s.

RESULTS

From 1996 to 2007 we caught 7,762 rodents belonging to 15 species: 10 granivorous species (*Chaetodipus nelsoni* [CHNE], *Chaetodipus penicillatus* [CHPE], *Dipodomys merriami* [DIME], *Dipodomys nelsoni* [DINE], *Dipodomys ordii* [DIOR], *Perognathus flavus* [PGFL], *Peromyscus eremicus* [PEER], *Peromyscus maniculatus* [PEMA], *Reithrodontomys fulvescens* [REFU], and *Reithrodontomys megalotis* [REME]), 2 folivores (*Neotoma albigula* [NEAL] and *Sigmodon hispidus* [SIHI]), 1 carnivorous species (*Onychomys torridus* [ONTO]), and 2 omnivorous sciurids (*Spermophilus mexicanus* [SPME] and *Spermophilus spilosoma* [SPSP]). The range of body mass of these species was from 6 g (PGFL) to 282 g (NEAL).

Density of rodents differed significantly across years ($F_{11,11} = 20.53$, $P < 0.001$), seasons ($F_{1,11} = 14.03$, $P = 0.003$), and habitats ($F_{1,11} = 238.03$, $P < 0.001$). There were no significant interactions. The lowest density was 8.0 rodents/ha in 1999 and the highest was 29.3 rodents/ha in 2004. Spring densities (14.2 ± 2.1 rodents/ha) were lower than fall densities (17.5 ± 2.1 rodents/ha). Density of rodents in shrub habitat (22.6 ± 1.7 rodents/ha) were higher than for grass habitats (9.1 ± 1.5 rodents/ha).
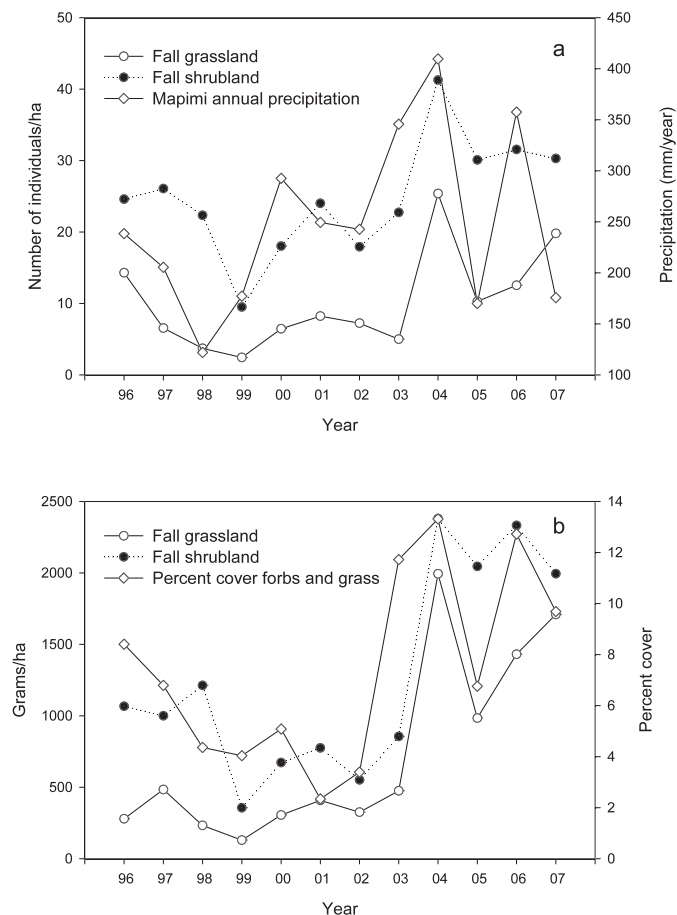
The biomass of rodents also differed by year ($F_{1,11} = 36.06$, $P < 0.001$), season ($F_{1,11} = 30.86$, $P < 0.001$), and habitat ($F_{1,11} = 81.27$, $P < 0.001$). There were also no significant interactions. Annual biomass averaged 848.3 ± 156.1 g/ha with a minimum of 343.0 g/ha in 1999 and a maximum of 1,691.8 g/ha in 2005. The biomass in shrub habitat was higher than in grassland (1,094.3 ± 165.7 g ha^{-1} year^{-1} versus 600.9 ± 119.4 g ha^{-1} year^{-1}). Fall biomass was higher than spring biomass (999.7 ± 191.8 g/ha versus 695.6 ± 153.3 g/ha).
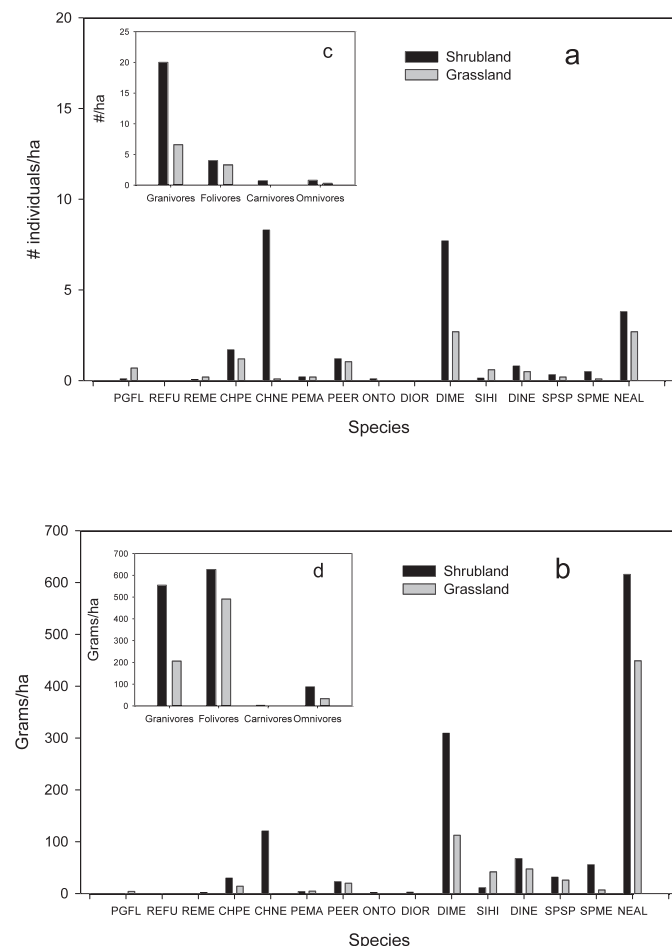
FIG. 1.—Density and biomass of a and b) individual species and c and d) of functional groups of rodent communities in grassland and shrubland habitats at the Mapimí study area. Data are overall averages from 12 years and across sample dates (spring and fall). See text for translation of individual species codes.

FIG. 2.—Annual changes in a) density and b) biomass of rodent communities in spring and fall and within grassland and shrubland habitats. Annual changes in a) precipitation and b) combined percent cover of forbs and grass are included for comparison with density and biomass changes.

Numeric and biomass distribution.—When averaged over the years and across seasons, most species were not very abundant nor did they contribute much to total community biomass (Fig. 1). In the shrubland habitat CHNE and DIME were the numerically dominant species, and in the grassland the dominant species were DIME and NEAL (Fig. 1a). On a biomass basis, because of its small size (14.6 ± 0.08 g, $n = 1,728$), CHNE was a minor species in the shrubland (Fig. 1b). Although DIME (40.8 ± 0.01 g, $n = 2,504$) was still prevalent in both habitats, NEAL (165.3 ± 0.04 g, $n = 1,212$) became the most dominant species (Fig. 1b) in both. Relative to functional groups, granivore species dominated in density (Fig. 1c), but folivores, specifically NEAL, dominated in biomass (Fig. 1d). In both habitats omnivores (SPSP and SPME) and the 1 carnivore species (ONTO) were minor in density and biomass (Fig. 1).

Changes in density and biomass over time.—The lowest total density and biomass values for both habitats were in 1999, and the highest were in 2004 (Fig. 2). In general, density and biomass levels were higher in the last 4 years of the study and corresponded to increases in annual precipitation

and forb and grass cover (Fig. 2). The species-specific contributions to density and biomass also changed over the years, but in different patterns. Except for differences in density between habitats, the species-specific contributions to total community density within both habitats did not show any major trends over time. The majority of the density was distributed mainly among 2 or 3 species over all the years of the study (Fig. 3). The contribution of minor species to density varied, with different individual species contributing more or less over time. For example, SIHI, which was absent from most samples in previous years, quickly rose to 27.4% of the total density in the grassland habitat in 2004 but literally disappeared from the samples the following years (Fig. 3).

In contrast to density, the distribution of biomass among the species showed a definite directional change over time. In a similar pattern as density, biomass initially was divided among several codominant species (Fig. 4). However, toward the later years of the study a majority of the biomass became concentrated in first 2, and then finally 1, dominant species (NEAL; Fig. 4). Also, the sudden increases in density of many minor species were not reflected in corresponding biomass increases because of their predominately small body sizes. For
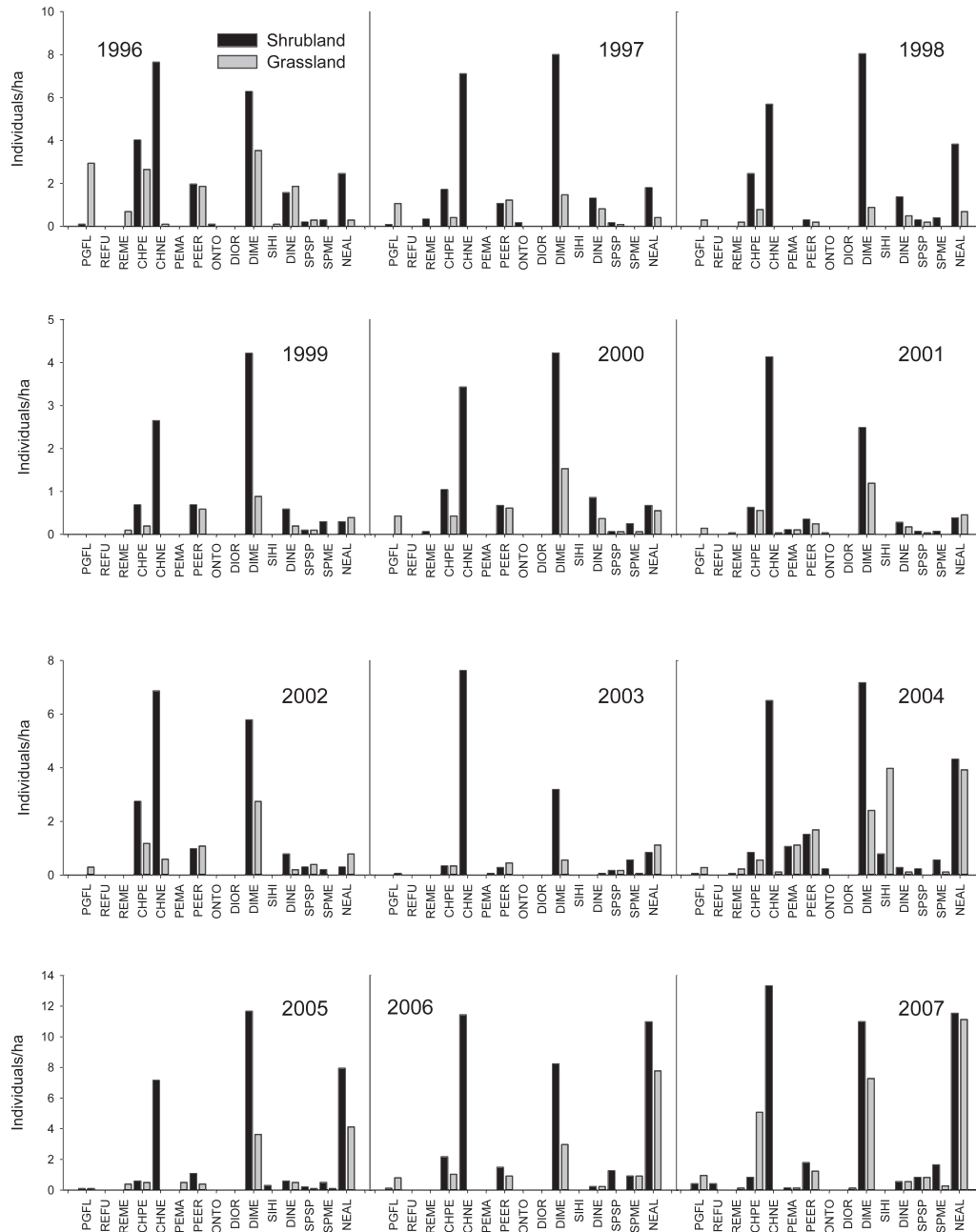
Fig. 3.—Annual species-specific changes in density in rodent communities for grassland and shrubland habitats over the length of the study (12 years). See text for translation of individual species codes.

example, PEER rose to 11.6% of the density in grasslands in 2004 but represented only 2.8% of the total biomass.

When we regressed the proportion of the total density that was concentrated in the top 2 species (DIME and CHNE) against total density (Fig. 5), the proportion contributed by the top 2 species declined as density increased (Fig. 5a). In contrast, as total biomass increased, the proportion contributed by the combined top 2 species (DIME and NEAL) rose to almost 80% (Fig. 5b). When considered alone, the top species (NEAL) contributed up to 60% of the total biomass at the higher biomass levels (Fig. 5b).

When we compared the density of granivores and folivores over the years of the study, we found that although folivore density increased during the last 4 years of the study in both habitats, granivores still remained the dominant numerical functional group (Figs. 6a and 6b). However, on the basis of biomass, what were predominately granivore communities early in the study switched to predominately folivore communities toward the end of the study (Figs. 6c and 6d).

Impact of precipitation and plant productivity.—Twelve-month precipitation amounts varied over the years of the study from 122 mm in 1998 to 407 mm in 2004 (Fig. 2a). Precipitation amounts did not differ between habitats (Hernández et al. 2005). Percent forb cover also varied over the years ($F_{10,10} = 5.98$, $P = 0.005$) and between seasons ($F_{1,10} = 25.83$, $P < 0.001$) but not between habitats. Grass cover did
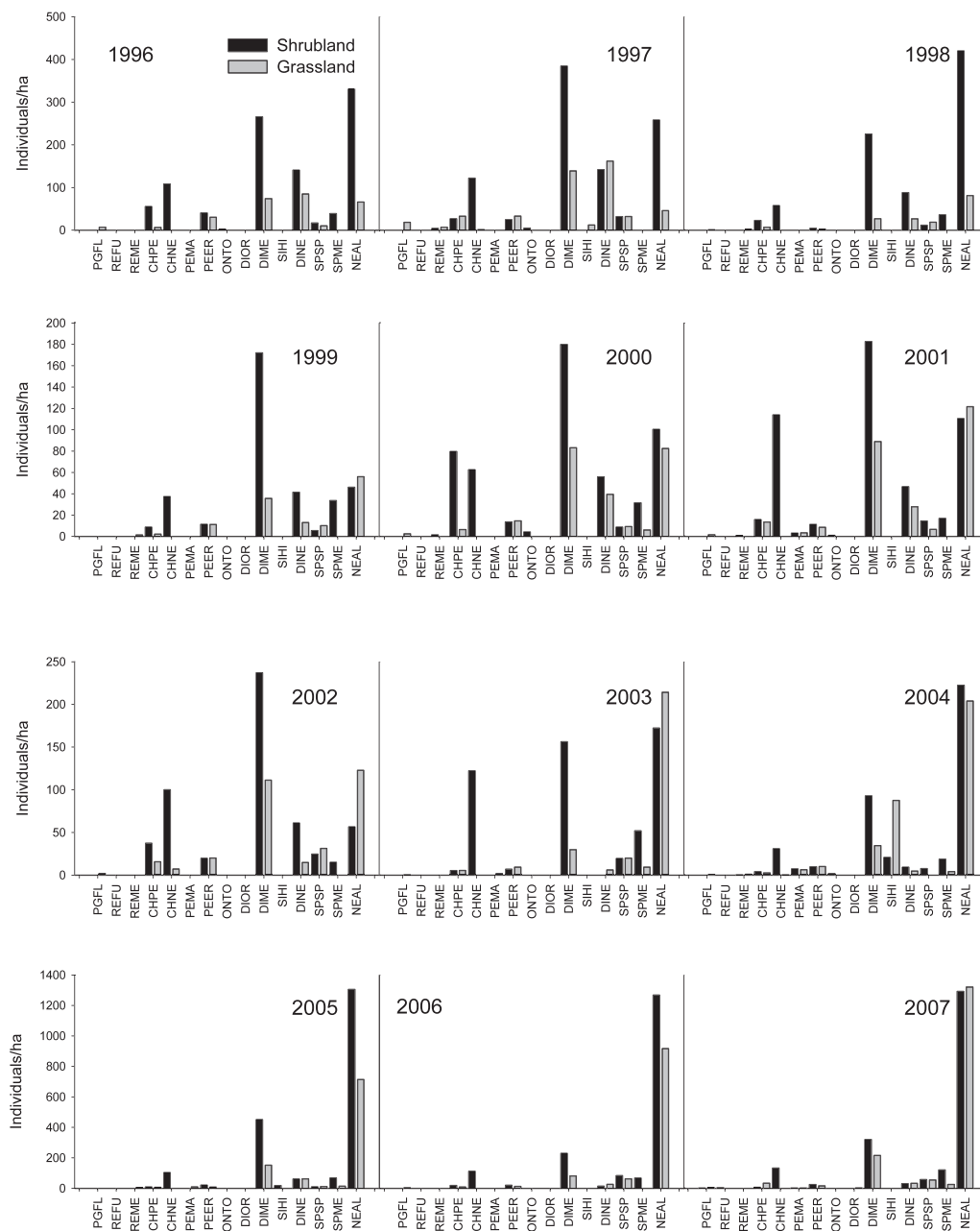
FIG. 4.—Annual species-specific changes in biomass in rodent communities for grassland and shrubland habitats over the length of the study (12 years). See text for translation of individual species codes.

not differ significantly among years nor season but did differ between habitats (10.50% ± 0.98% for grassland versus 0.26% ± 0.09% for shrubland: $F_{1,10} = 95.62$, $P < 0.001$).

Total rodent densities and biomass in fall were not significantly related to the previous 12-month precipitation amounts. However, total densities and biomass were related to the 12-month amounts received a year prior to the sample dates (densities: $F_{1,10} = 10.52$, $P = 0.009$, $r^2 = 0.46$; biomass: $F_{1,10} = 7.46$, $P = 0.021$, $r^2 = 0.37$). Spring densities and biomass were significantly related to the previous 12-month precipitation amounts (densities: $F_{1,10} = 17.97$, $P = 0.002$, $r^2 = 0.61$; biomass: $F_{1,10} = 10.78$, $P = 0.008$, $r^2 = 0.47$). Individual densities and biomass of the 2 main functional

groups, granivores and folivores, also were significantly related to corresponding precipitation amounts for fall and spring (for granivores, fall density: $F_{1,10} = 8.09$, $P = 0.017$, $r^2 = 0.39$; spring density: $F_{1,10} = 18.46$, $P = 0.002$, $r^2 = 0.61$; fall biomass: $F_{1,10} = 8.86$, $P = 0.014$, $r^2 = 0.42$; spring biomass: $F_{1,10} = 12.61$, $P = 0.005$, $r^2 = 0.51$; for folivores, fall density: $F_{1,10} = 6.41$, $P = 0.03$, $r^2 = 0.33$; spring density: $F_{1,10} = 7.25$, $P = 0.023$, $r^2 = 0.36$; fall biomass: $F_{1,10} = 5.62$, $P = 0.039$, $r^2 = 0.30$; spring biomass: $F_{1,10} = 6.95$, $P = 0.025$, $r^2 = 0.35$).

Total density and biomass of rodents for fall and spring were significantly related separately to percent cover of forbs and grasses. To analyze how total usable plant productivity—
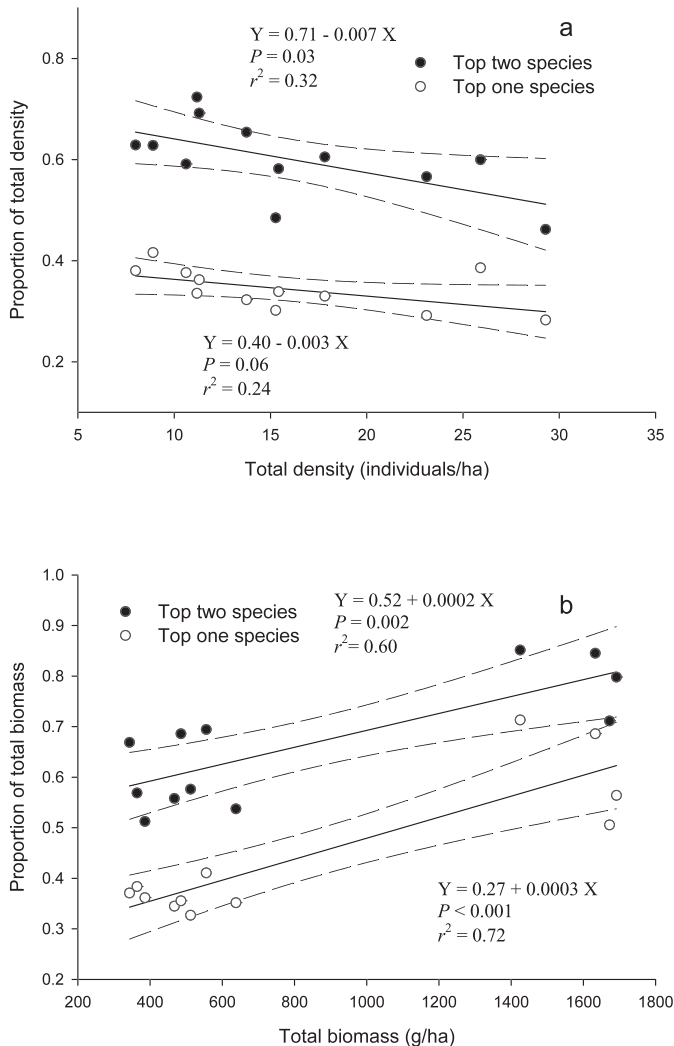
FIG. 5.—Relationships between the proportional contribution of the top 2 and 1 species to a) total density or b) biomass of the rodent community in the Mapimí study area. The dashed lines are 95% confidence intervals around the regression line, and the r^2 values are adjusted for sample sizes.

that is, grass and forbs—might affect rodent density and biomass we summed the percent cover of grass and forbs for the following analyses. In these analyses total rodent density and biomass in fall were significantly related to combined percent cover of grass and forbs from the previous fall for the grassland but not the shrubland habitat (Figs. 7a and 7b). For spring, the relationship between total rodent density or biomass and combined forb and grass cover from the previous fall were significant for both habitat types (Figs. 8a and 8b). Although the relationships between density and biomass of granivores and folivores varied between habitats and seasons (Figs. 7 and 8), the patterns seen for density and biomass were similar. For example, when the relationship between spring density of folivores in the shrubland was not significant (Fig. 8c), the relationship for biomass also was not significant (Fig. 8d). When the relationship between cover and density for granivores and folivores was highly significant (e.g., Fig. 8e), it also was highly significant for biomass (Fig. 8f).

DISCUSSION

Our analyses investigated 2 metrics of rodent communities, density and biomass, and how closely they are related. Based on our results, changes in total density and biomass paralleled each other closely. Also, these changes in density and biomass seem to be affected similarly by bottom-up forces of precipitation and resulting plant productivity. These similar responses extended across 2 different habitats and seasons. When density exhibited a strong relationship with plant cover—for example, grasslands in the spring—an equally strong relationship was found for biomass. As with density, fall biomass levels were not related to same-year precipitation and primary productivity levels but exhibited a year lag time commonly found in other studies (Ernest et al. 2000; Hernández et al. 2005). This relationship appears habitat dependent, being significant only in the grassland habitat, again for both density and biomass. Both spring density and biomass were highly related to plant productivity in the previous season for both habitats. The strength of the relationship indicates that an increase in the plant productivity of a given growing season has its strongest positive effect not on same-season reproduction but on the survival of individuals over the subsequent winter or dry period. This effect possibly contributes to the lag noted by influencing the number of individuals available for reproduction the subsequent breeding season.

The overall outcome of these comparisons indicated that analyses of either density or biomass would produce similar results regarding how the bottom-up factors of precipitation and plant productivity would affect rodent community dynamics. This similarity persisted when we divided the community into its dominant functional groups. Top-down forces of predation and competition are known to play a role in species density (Meserve et al. 2003), although their extent is unclear (Previtali et al. 2009). Because we did not have data to directly test for top-down effects, we cannot speculate as to whether these effects would be similar for density and biomass.

Although we found concordance between changes in total density and total biomass estimates regarding impacts of precipitation and plant cover, we did find differences in how total density and biomass were distributed among the species within the community and how they changed over time. Rodent communities commonly are dominated numerically by a few species, with the rest of the members playing minor roles (Ernest 2005; Ernest and Brown 2001; Hernández et al. 2005). When we considered community structure based on species-specific biomass contributions, we also found a few species dominating. However, the species dominating numerically need not be the same as those dominant in biomass. In the shrubland habitat CHNE changed from a dominant species numerically to a low-ranking species based on biomass. NEAL, on the other hand, was the 3rd- and 2nd-ranking numerical species in the shrubland and grassland, respectively, but became the dominant species in both habitats on the basis of biomass. This shift in dominance also was prevalent on the basis of the functional roles of species. Granivores dominated numerically in both habitats, but folivores exceeded them based on biomass.
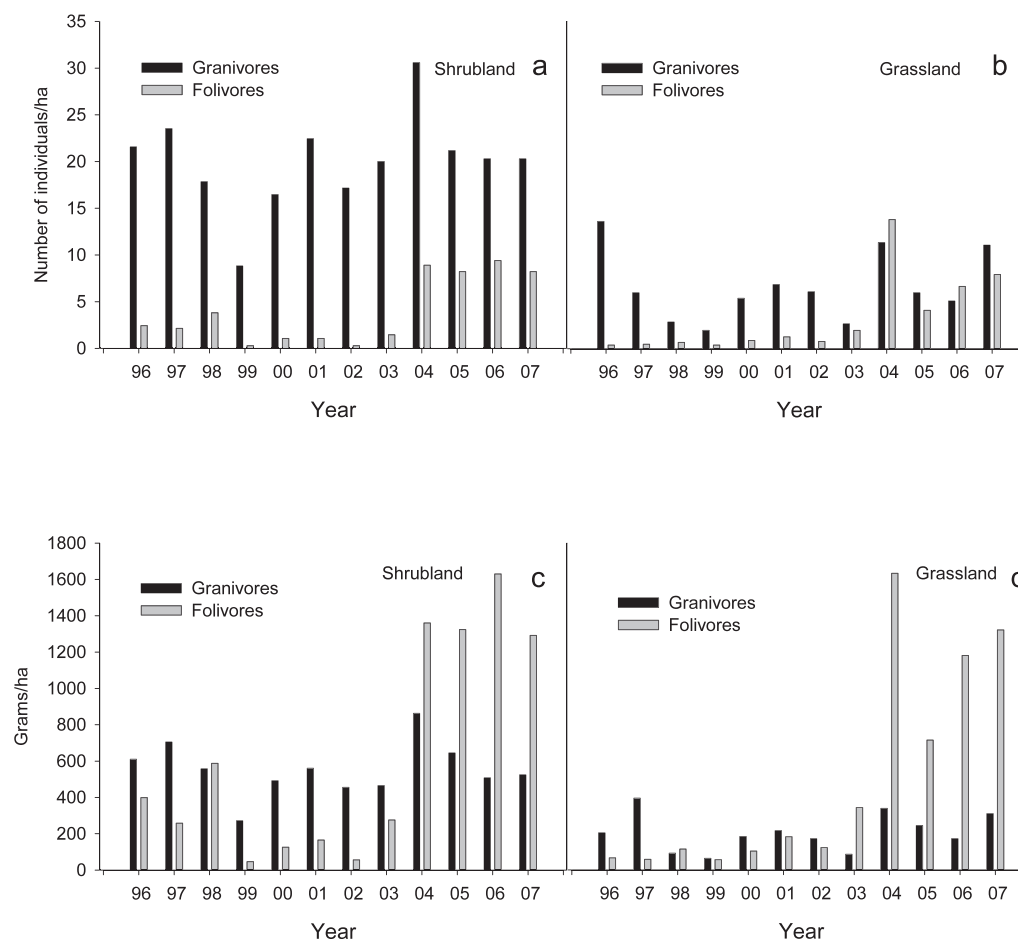
FIG. 6.—Annual a and b) density and c and d) biomass of granivore and folivore species in the grassland and shrubland habitats of the Mapimí study area. The data are from fall samples.

This discrepancy between density and biomass became more obvious when we considered species-specific changes over time. Species-specific contributions to both density and biomass indicated a very dynamic rodent community over the 12 years of the study. However, how to interpret the effects of these changes on community structure depended on the parameter considered. Based on densities of individual species, examination of our data indicated a decline in the proportion of the top numerical species as total density increased. This would signify that under favorable conditions—for example, increased precipitation and food resources—the rodent community becomes increasingly diverse, with all species, especially minor ones, benefiting from increased primary productivity. This appeared evident when the density of most species increased in years with more favorable conditions; for example, 2004. However, what appeared to be an increasingly diverse community based on species density was becoming simpler relative to the distribution of biomass among the species. When the total biomass was high, >80% of the biomass was tied up in just 2 species, and most of that (60%) was in 1 species (NEAL). Also, biomass in both habitats became more concentrated in NEAL toward the end of the study.

Aside from the total biomass distribution becoming less diverse, a major shift in the proportion of biomass also occurred in the functional groups. Examination of density data indicated that granivore species maintained their dominance throughout the study. However, on a biomass basis, the rodent community changed to one dominated by the folivore NEAL.

Based on our results, density alone did not accurately reflect the role each species or functional groups played in the distribution of biomass within the rodent community. Also, density did not provide accurate insights as to how those biomass roles were affected by changes in precipitation and primary productivity. As conditions improved, density data indicated a robust diverse rodent community, as is commonly found in many communities. However, in relation to biomass, most of the biomass of the community was becoming concentrated in fewer species.

What are the ramifications of these differences between density and biomass distribution within the community? Many analyses of rodent community structure are limited to either strictly granivorous species or to the density of species (Ernest and Brown 2001; Thibault et al. 2004; White et al. 2004). However, we found a large-bodied, but numerically subordinate, folivore (NEAL) dominating the biomass contribution, whereas a numerically dominant but small granivore (CHNE) did not contribute significantly to biomass levels. This indicates that we should be cautious in using only numerical
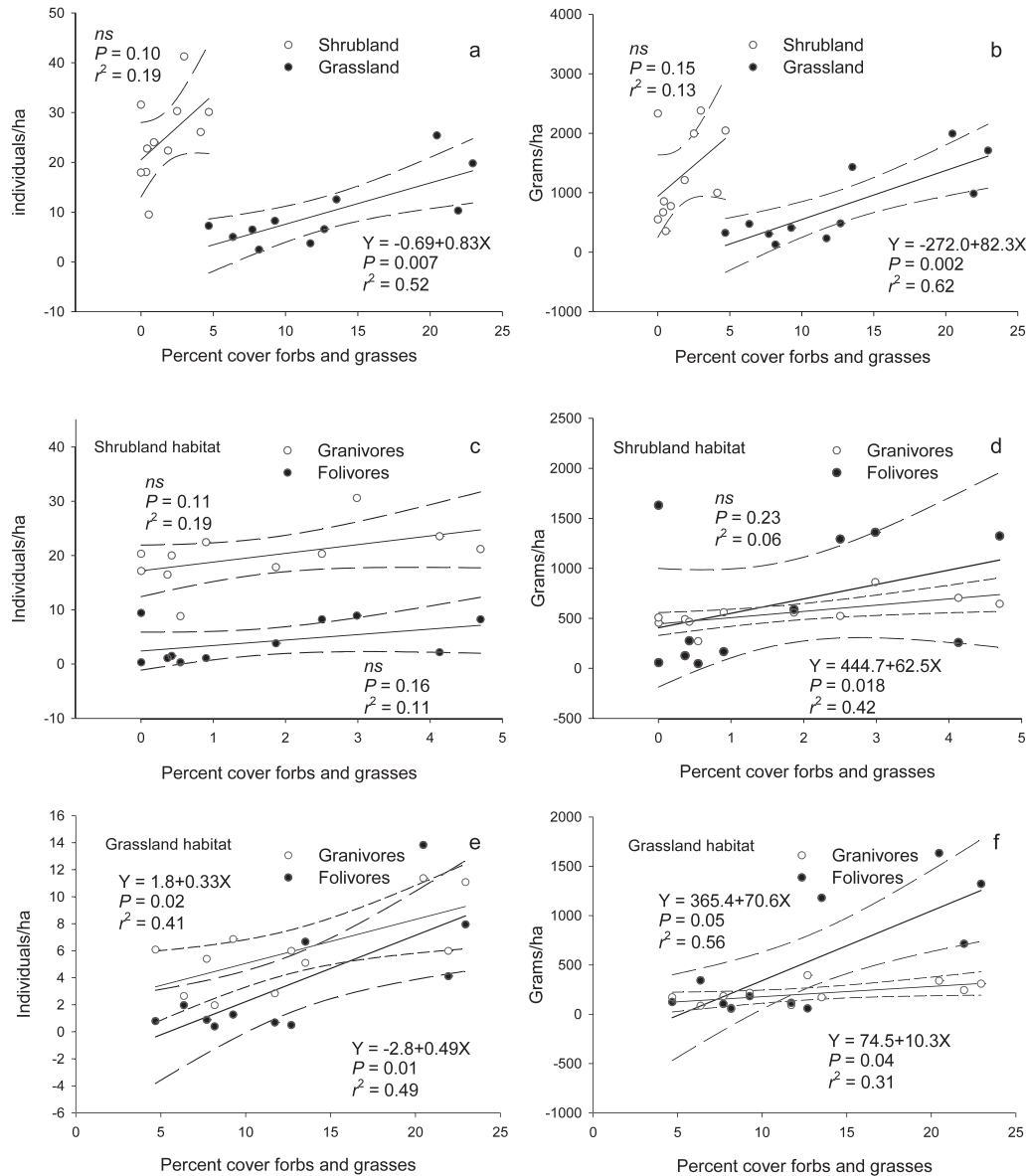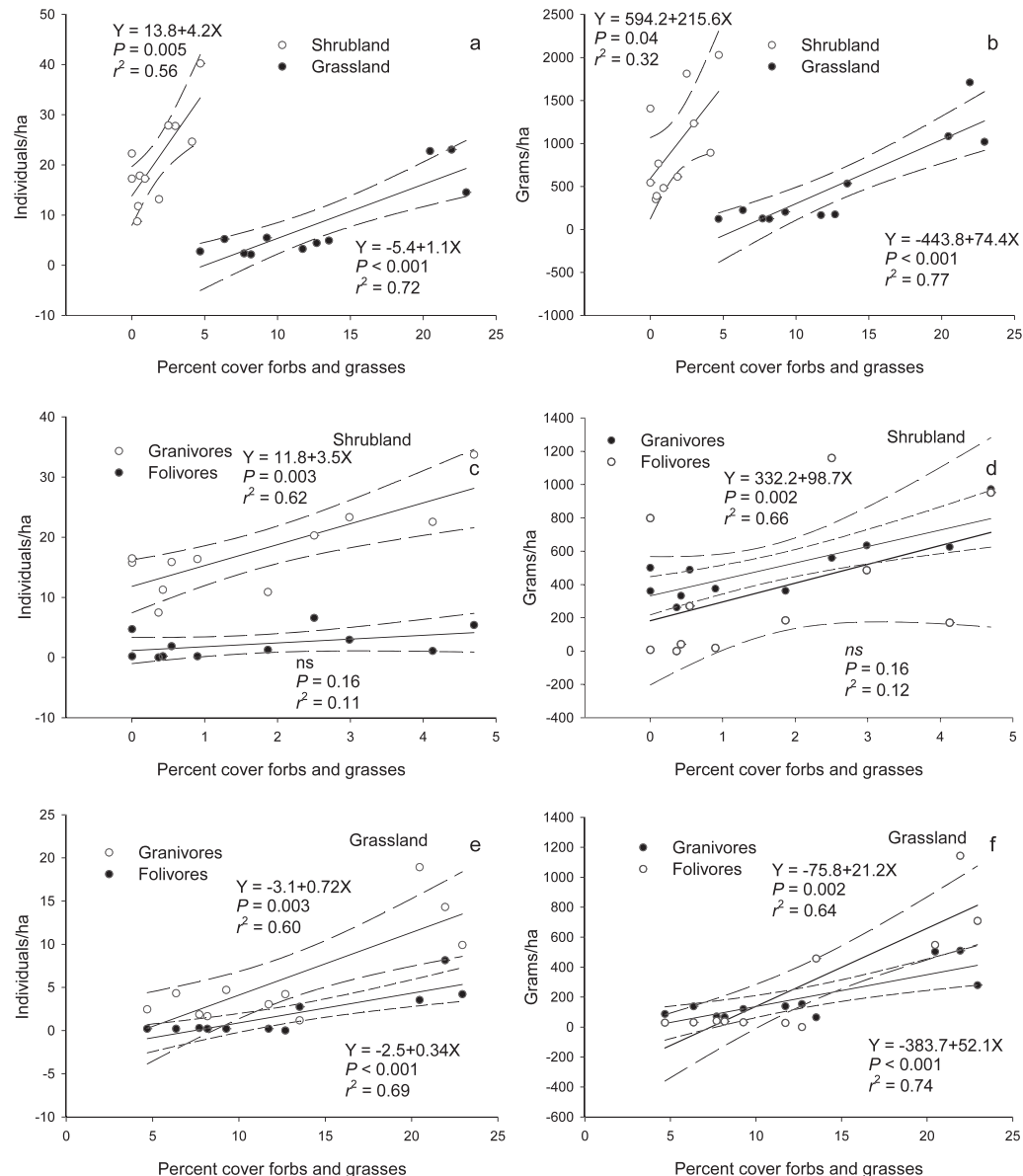
FIG. 7.—a and b) Relationships of density and biomass in the fall to percent cover of forbs and grasses of the previous fall for shrub and grassland habitats. Relationships of c and e) fall density and d and f) biomass of the granivore and folivore groups to percent forb and grass cover of the previous fall. The dashed lines are 95% confidence intervals around the regression line, and the r^2 values are adjusted for sample sizes.

density as an indicator of the importance of a species within a community. For example, in Arizona White et al. (2004) reported a reduction in mean body mass because smaller-bodied species (CHPE and *C. baileyi*) increased to ~20% of the population. However, even with increases in these smaller species, total biomass still was dominated by larger species (DIME and DIOR), which made up >60% of the community numerically (Ernest and Brown 2001) and >80% of the total biomass (based on our calculations applied to the findings of Ernest and Brown [2001], Lima et al. [2008], and White et al. [2004]). Thus, the numerical distribution of individual body sizes might be an important property of the community (White et al. 2004), but its role has to be considered in reference to the contribution each size category makes to overall biomass availability. As we found in our study, increases in density of

smaller-bodied species did not contribute significantly to increases in biomass levels.

Why is the distribution of body size biomass important? As with body size distributions (Ernest 2005), analyses of distributions of body size biomass can provide insight into how bottom-up forces possibly affect structuring rules of communities (Ernest 2005; White et al. 2004). Primary production available to the rodent community in the desert environment consists mainly of green forage and seeds. The predominance of granivore biomass in the earlier, drier time of our study indicated that seed production was the most important energy source for the rodent community at that time. However, later in the study the dominance of folivores indicated a significant shift to a community based more on green plants. We suggest that changes in forb production were

Fig. 8.—a and b) Relationships of density and biomass in the spring to percent cover of forbs and grasses of the previous fall for shrub and grassland habitats. Relationships of c and e) spring density and d and f) biomass of the granivore and folivore groups to percent forb and grass cover of the previous fall. The dashed lines are 95% confidence intervals around the regression line, and the r^2 values are adjusted for sample sizes.

in large part responsible for this shift. Early in the study, when precipitation levels were at or below the long-term average, forb cover was minimal (<1%) but seed-producing grasses persisted. In the later, wetter years of the study forb production increased to as much as 4% cover. Although a 4% increase in forb production might not appear to be important, it represents a 400% increase over dry years. This appearance of forbs provided highly nutritious plant material for folivore species such as NEAL and SIHI. In fact it is in the years of highest forb production (2003–2004) when NEAL became the dominant biomass species and SIHI suddenly reappeared in our samples as the 2nd ranking biomass species in the grassland habitat. Consequently, as energy pathways from the primary producer level change, it appears that they can have significant impacts on rodent community structure.

The implication of these changing pathways is that evolutionarily derived foraging strategies of individual species and functional groups such as granivores and folivores can significantly affect the impact of bottom-up forces on rodent community dynamics. Within a functional group the role of interspecific competition normally has been emphasized as a factor affecting group structure. However, even in closely related species, differences in handling times, encounter rates, and harvest rates of different food resources and giving-up densities and antipredator abilities are the basic mechanistic factors that affect competitive interactions and produce the ultimate superficial competitive results we see in the field (Brown 1989a). Consequently, as food resources change, much of the resulting changes in species-specific density and corresponding biomass distribution can be attributed to

species-specific foraging strategies, predation risk, and the actual feeding opportunities available. The view that species' contributions within a functional group change primarily through competitive interactions, where one species wins at the expense of another, overshadows the importance of these differences in foraging strategies and opportunities. The role of these factors becomes more obvious between functional groups, where changes in relative contributions to the overall rodent community, as noted in this study, cannot be explained simply by competitive interactions. However, even within a given functional group, subtle differences in evolutionary adaptations to foraging and predator avoidance can have significant impacts on a species' access to primary productivity pathways and determine its status within the community relative to both density and biomass. This can complicate the predicted response of species to changes in competitive interactions, such as the removal of competing species (Brown and Munger 1985).

By including more detailed information on types of food resources available and foraging strategies and predator–prey interactions into studies of rodent community structure, it may be possible to better delineate their roles in structuring communities. Testing predictions of how changes in the availability of different-sized seed resources will impact granivore community structure, or how altering the proportion of safe versus risky habitat in the rodents' landscape of fear (Laundré et al. 2010) will impact relative species density and biomass distributions, could prove beneficial in expanding our understanding of community dynamics.

The distribution of body-size biomass is important also because a major function of the rodent community is to provide energy in the form of biomass to the subsequent mesocarnivore community. Members of this community vary in size and hunting strategies and, consequently, preferred diets (Delibes et al. 1989). Because of these diet differences, increases in total density and biomass of rodents might or might not translate into increased energy for all members of the mesocarnivore community. For example, frequency of occurrence of rodents in the scats of coyotes (*Canis latrans*) in the Chihuahuan Desert is ~30% (Hernández et al. 2002; Laundré et al. 2009). In our study area a large proportion of the rodents consumed by coyotes, on average ~14% occurrence in feces, was NEAL (Hernández et al. 2002; Laundré et al. 2009). Increases in biomass of this large-bodied species obviously would benefit coyotes more than smaller predators who feed primarily on smaller rodents (Delibes et al. 1989). During the years of higher biomass availability of NEAL in our study area percent occurrence of this species in coyote scats rose to 25–34% (Laundré et al. 2009). An analysis of just a portion of the rodent community (e.g., granivores) or of just the relative species densities would miss or obscure this shift in the amount and form of energy availability in the community.

In conclusion, in addition to affecting density of species, primary productivity appears to alter the species makeup and biomass contribution of the rodent community. In our study area higher food availability had the paradoxical effect of increasing species-specific densities and at the same time simplifying the community on a biomass basis. Such changes in the distribution

of biomass potentially can have cascading impacts on both higher and lower trophic levels. These results illustrate the need to expand our studies of traditional density distribution to include analyses of biomass distribution of all functional groups of rodent communities. Recent studies of this type have been enlightening (Ernest 2005; Thibault et al. 2004). Additional studies, especially of how the various axes of environmental heterogeneity (Brown 1989a, 1989b) affect energy pathways through the rodent community, will increase our understanding of the basic dynamics of this important community in the Chihuahuan Desert.

RESUMEN

Varios trabajos, especialmente en ecosistemas áridos, han estudiado las dinámicas poblacionales y de comunidades de roedores. La mayoría de estos estudios se han enfocado en entender los cambios a través del tiempo de las densidades de roedores de especies particulares o de todas las especies en su conjunto. La contribución en biomasa de cada especie es un factor importante en cuanto a la energía disponible para la comunidad de meso-carnívoros. Pese a que la biomasa y la densidad están relacionadas, no se ha dado mucha atención sobre posibles diferencias entre ellas y sobre la importancia de estas diferencias sobre la estructura y función de las comunidades. En este estudio analizamos datos de 12 años de densidades y biomasa de roedores en el Desierto Chihuahuense en el norte de México. Los datos se colectaron anualmente en primavera y otoño, se usaron trampas para roedores vivos colocadas de manera radial. La densidad y biomasa cambiaron significativamente de manera paralela año con año, y ambas estuvieron relacionadas con la precipitación y el porcentaje de cobertura de pastos y herbáceas. Con base en la densidad y la biomasa, la comunidad de roedores estuvo dominada por 2 o 3 especies principales. Sin embargo a nivel específico de especie, la especie numéricamente dominante fue la granívora pequeña (*Chaetodipus nelsoni*), en tanto que la folívora de gran tamaño (*Neotoma albigula*) dominó en biomasa. Mientras que la densidad total incrementó, la proporción con la que contribuyó la especie dominante disminuyó. Por su parte, cuando incrementó la biomasa total, también la proporción de las 2 especies dominantes incrementó en un 80% de la biomasa total. Durante los 12 años de este estudio, la distribución de las especies basada en la densidad no mostró un cambio en dirección. En cambio, la biomasa de la comunidad de roedores se concentró gradualmente en una sola especi folívora, *N. albigula*. Pese a que la densidad y biomasa totales respondieron de manera similar a la precipitación y a la productividad vegetal, existen diferencias considerables entre estas 2 características y las contribuciones específicas de cada especie a los cambios dentro de la comunidad. Se presenta una discusión sobre el significado de estas diferencias en relación a las estrategias de forrajeo y la variación de las oportunidades de alimentación dentro de la comunidad.

LITERATURE CITED

BROWN, J. H., AND S. K. M. ERNEST. 2002. Rain and rodents: complex dynamics of desert consumers. BioScience 52:979–987.

BROWN, J. H., S. K. M. ERNEST, J. P. PARODY, AND J. P. HASKELL. 2001. Regulation of diversity: maintenance of species richness in changing environments. Oecologia 126:321–332.

BROWN, J. H., AND E. J. HESKE. 1990. Temporal changes in a Chihuahuan Desert rodent community. Oikos 59:290–302.

BROWN, J. H., AND J. C. MUNGER. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. Ecology 66:1545–1563.

BROWN, J. S. 1989a. Desert rodent community structure: a test of four mechanisms of coexistence. Ecological Monographs 59:1–20.

BROWN, J. S. 1989b. Mechanisms underlying the organization of a desert rodent community. Journal of Arid Environments 17:211–218.

BROWN, J. S., B. P. KOTLER, AND W. A. MITCHELL. 1994. Foraging theory, patch use, and the structure of a Negev Desert granivore community. Ecology 75:2286–2300.

CORNET, A. 1988. Principales caracteristiques climatiques. Pp. 45–76 in Estudio integrado de los recursos vegetacion, suelo y agua en la Reserva de la Biosfera de Mapimi. I. Ambiente natural y humano (C. Montaña, ed.). Instituto de Ecología, A.C., Xalapa, Veracruz, México D. F. Publicación 23.

DELIBES, M., L. HERNÁNDEZ, AND F. HIRALDO. 1989. Comparative food habits of three carnivores in western Sierra Madre, Mexico. Zeitschrift für Säugetierkunde 54:107–110.

ERNEST, S. K. M. 2005. Body size, energy use, and community structure of small mammals. Ecology 86:1407–1413.

ERNEST, S. K. M., AND J. H. BROWN. 2001. Homeostasis and compensation: the role of species and resources in ecosystem stability. Ecology 82:2118–2132.

ERNEST, S. K. M., J. H. BROWN, AND R. R. PARMENTER. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. Oikos 88:470–482.

FLOMBAUM, P., AND O. E. SALA. 2007. A non-destructive and rapid method to estimate biomass and aboveground net primary production in arid environments. Journal of Arid Environments 69:352–358.

FLOYD, D. A., AND J. E. ANDERSON. 1982. A new point frame for estimating cover of vegetation. Vegetatio 50:185–186.

GANNON, W. L., R. S. SIKES, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

GIOVANNI, M. D., C. W. BOAL, AND H. A. WHITLAW. 2007. Prey use and provisioning rates of breeding Ferruginous and Swainson's hawks on the southern Great Plains, USA. Wilson Journal of Ornithology 119:558–569.

HERNÁNDEZ, L., A. GONZÁLEZ-ROMERO, J. W. LAUNDRÉ, D. LIGHTFOOT, E. ARAGÓN, AND J. LÓPEZ-PORTILLO. 2005. Changes in rodent community structure in the Chihuahuan Desert Mexico: comparisons between two habitats. Journal of Arid Environments 60:239–257.

HERNÁNDEZ, L., R. R. PARMENTER, J. W. DEWITT, D. C. LIGHTFOOT, AND J. W. LAUNDRÉ. 2002. Coyote diets in the Chihuahuan Desert, more evidence for optimal foraging. Journal of Arid Environments 51:613–624.

KOTLER, B. P., J. S. BROWN, AND W. A. MITCHELL. 1993. Environmental factors affecting patch use in two species of gerbilline rodents. Journal of Mammalogy 74:614–620.

LAUNDRÉ, J. W., J. M. M. CALDERAS, AND L. HERNÁNDEZ. 2009. Foraging in the landscape of fear, the predator's dilemma: where should I hunt? Open Ecology Journal 2:1–6.

LAUNDRÉ, J. W., L. HERNÁNDEZ, AND W. J. RIPPLE. 2010. The landscape of fear: ecological implications of being afraid. Open Ecology Journal 3:1–7.

LIMA, M., S. K. M. ERNEST, J. H. BROWN, A. BELGRANO, AND N. C. STENSETH. 2008. Chihuahuan Desert kangaroo rats: nonlinear effects of population dynamics, competition, and rainfall. Ecology 89:2594–2603.

MESERVE, P. L., D. A. KELT, W. B. MILSTEAD, AND J. R. GUTIÉRREZ. 2003. Thirteen years of shifting top-down and bottom-up control. BioScience 53:633–646.

MURRAY, B. R., AND C. R. DICKMAN. 1994. Granivory and microhabitat use in Australian desert rodents: are seeds important? Oecologia 99:216–225.

PARMENTER, R. R., ET AL. 2003. Small-mammal density estimation: a field comparison of grid-based vs web-based density estimators. Ecological Monographs 73:1–26.

PREVITALI, M. A., M. LIMA, P. L. MESERVE, D. A. KELT, AND J. R. GUTIÉRREZ. 2009. Population dynamics of two sympatric rodents in a variable environment: rainfall, resource availability, and predation. Ecology 90:1996–2006.

REICHMAN, O. J. 1975. Relation of desert rodent diets to available resources. Journal of Mammalogy 56:731–751.

THIBAULT, K. M., E. P. WHITE, AND S. K. M. ERNEST. 2004. Temporal dynamics in the structure and composition of a desert rodent community. Ecology 85:2649–2655.

WANG, G., Q. ZHOU, W. ZHONG, C. SUN, AND Z. CHEN. 2001. Species richness–primary productivity relationship of plants and small mammals in the Inner Mongolian steppes, China. Journal of Arid Environments 49:477–484.

WHITE, E. P., S. K. M. ERNEST, AND K. M. THIBAULT. 2004. Trade-offs in community properties through time in a desert rodent community. American Naturalist 164:670–676.