

Bottom-up regulation of desert grassland and shrubland rodent communities: implications of species-specific reproductive potentials

DAVID C. LIGHTFOOT,* ANA D. DAVIDSON, DARA G. PARKER, LUCINA HERNÁNDEZ, AND JOHN W. LAUNDRÉ

Department of Biology MSC 2020, The University of New Mexico, Albuquerque, NM 87131, USA (DCL, ADD)

Instituto de Ecología, Universidad Nacional Autónoma de México, México, Distrito Federal, México (ADD)

Department of Biology MSC 3AF, New Mexico State University, Las Cruces, NM 88003, USA (DGP)

Department of Biological Sciences, 316 Snygg Hall, State University of New York, Oswego, NY 13126, USA (LH, JWL)

* Correspondent: dlightfo@unm.edu

We conducted an 11-year comparative study on temporal variation in rodent density, biomass, and species composition dynamics from adjacent grassland and shrubland environments in the Chihuahuan Desert of North America, in relation to rainfall and plant production. We found that rodent assemblages from those environments were only 14% similar in overall species composition, but consisted of different species in the same genera with similar ecological attributes. Each rodent community was numerically dominated by a different species of granivorous kangaroo rat, and the 2 rodent communities paralleled each other in body sizes and trophic structure. Rodent species compositions changed little over the 11-year period, despite considerable variation in rodent densities and biomass and in rainfall and plant production. Rodent abundance and biomass from both communities increased in relation to temporally variable rainfall and plant production, especially resulting from a series of El Niño and La Niña Southern Oscillation events. However, the grassland rodent community exhibited more rapid within-1-year lag-time responses to plant production, and prolonged high densities for 1 year before declining, whereas the shrubland rodent community exhibited primarily 1-year lag responses and immediate rapid decline in densities. Changes in rodent densities and biomass from both communities were significantly predicted by the production of annual grasses and forbs. Measured rodent reproductive activity was greater and happened sooner after rain and plant production events at the grass site than at the shrub site, and differences in the timing of rodent bottom-up responses between the grassland and shrubland habitats appeared to result from differences in the reproductive potentials of the 2 dominant rodent species. *Dipodomys ordii*, the dominant grassland rodent species, is known to produce more offspring than *Dipodomys merriami*, the dominant rodent in the shrubland community. We conclude that differences in the reproductive potentials of these 2 dominant rodent species likely accounted for the quicker and prolonged response of the grassland rodent community to bottom-up influences, rather than differences in the timing of plant production between the sites. Variation in reproductive potentials among rodent communities is likely a key factor affecting the timing of overall rodent community dynamics relative to changes in environmental resources.

Key words: abundance, community composition, *Dipodomys*, El Niño–La Niña Southern Oscillation, kangaroo rats, plant production, population dynamics, rainfall

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DOI: 10.1644/11-MAMM-A-391.1

Arid and semiarid desert environments are water-limited systems where resources are highly variable in space and time (Noy-Meir 1985; Reynolds et al. 2004; Schwinning et al. 2004), and understanding the importance of bottom-up controls on consumer dynamics in desert systems has been of long-standing interest in ecology. Rodents are ecologically important consumers in arid regions throughout the world (Kelt et al. 1996; Reichman 1991), and in some systems are considered keystone species (Brown and Heske 1990a; Davidson and

Lightfoot 2006; Davidson et al. 2010; Kerley et al. 1997). Desert rodent densities are highly variable over space and time, and populations tend to respond positively to bottom-up controls of rainfall and increased food resources through increased plant production (Beatley 1969; Dickman et al. 2010;



Shenbrot et al. 2010; Stapp 2010; Thibault et al. 2010). However, some studies have found little (Ernest and Brown 2001) or even negative (Kelt et al. 2008; Thibault and Brown 2008; Valone and Brown 1995) effects of rainfall on desert rodent abundance.

Bottom-up regulation of desert rodent communities appears to be more complex than simple positive linear relationships between rainfall, plant production, and rodent densities (e.g., Brown and Ernest 2002; Kelt 2011; Lima et al. 2008; Thibault et al. 2010). This nonlinear complexity appears to be derived from variation in biotic and abiotic interactions (Brown and Ernest 2002; Ernest et al. 2000, 2008; Kelt 2011; Letnic et al. 2011; Meserve et al. 2003; Whitford and Steinberger 1989), which vary considerably both spatially and temporally among different habitats or environments across desert landscapes (Shenbrot et al. 2010). Additionally, different desert environments or habitats support different rodent communities because of habitat selection among rodent species (Rosenzweig and Abramsky 1985; Shenbrot et al. 2010). Rodent species have been found to exhibit different responses to bottom-up regulation, both within the same community or habitat (Brown and Heske 1990b; Previtali et al. 2009; Thibault et al. 2010), and between communities or habitats (Hernández et al. 2005, 2011; Shenbrot et al. 2010).

Interspecific interactions such as density-dependent resource competition are important factors structuring the species and functional guild composition of North American desert rodent communities (Davidson et al. 1985; Ernest and Brown 2001; Ernest et al. 2008; Fox and Brown 1993; Kelt 2011; Lima et al. 2008). Top-down effects of predation also are known to affect desert rodent communities (Kelt 2011; Kotler 1984; Kotler et al. 1988; Longland and Price 1991; Yunker et al. 2007). All of these factors along with habitat selection (Shenbrot et al. 2010) and rodent reproductive potentials (Brown and Harney 1993; Conley et al. 1977; Reichman and Van De Graff 1975; Whitford 1976) largely determine the rodent community species composition, trophic structure, and abundance in any given location.

Grasslands and shrublands are 2 of the most common vegetation types in semiarid regions throughout the world (Evaneri et al. 1985; Goodall et al. 1981), and each of these vegetation types tends to have different climate and soils associated with it (Le Houerou 1984; Muldavin et al. 2008; Whitford 2002). The individual plant and soil nutrient patterns of desert grasslands exhibit a fine spatial scale, and the shallow-rooted herbaceous perennial grasses grow rapidly in response to light rains. In contrast, desert shrublands are spatially coarse environments, with vegetation and soil nutrient resources patchily distributed across the landscape and deep-rooted woody perennial plants that respond to longer-term trends in deep soil moisture (Reynolds et al. 2004; Schlesinger et al. 1990). Consequently, aboveground net primary production (ANPP) of desert grasslands is better correlated with precipitation than in shrublands (Le Houerou 1984; Whitford 2002). Furthermore, both perennial and annual plant species, and those plants with C3, C4, or CAM photosynthetic

pathways, all codominate northern Chihuahuan Desert grasslands and shrublands, and respond differently to seasonal rainfall. Muldavin et al. (2008) found that summer rainfall caused rapid growth of shallow-rooted, C4-dominated black grama grassland vegetation; whereas winter rains caused spring growth of deep-rooted, C3 creosote bush shrublands.

If the soil, plant, and rainfall response dynamics of desert grasslands and shrublands are known to function differently, then the animal consumer dynamics also should differ. Bottom-up regulation of desert rodent communities has been studied mostly from desert shrublands (Reichman 1991), semiarid thorn scrub (Meserve et al. 2003), sandy environments (Dickman et al. 1999; Letnic et al. 2011; Shenbrot et al. 2010), and transitional shrub-grass locations (Brown and Heske 1990b; Thibault et al. 2010). Few studies have compared the temporal dynamics of rodent communities between desert grassland and shrubland environments. Hernández et al. (2005) tested the resource availability hypothesis relative to rodent abundance and diversity, comparing central Chihuahuan Desert piedmont slope shrublands to drainage basin grasslands, and found a shorter lag response of rodent density increases to rainfall in the grassland habitat. Ernest et al. (2000) examined northern Chihuahuan Desert piedmont slope grasslands and shrublands, and found that rodents increased in response to rainfall and plant production at the same rate in both habitats. These studies from different regions of the Chihuahuan Desert and in different types of shrublands and grasslands had inconsistent findings, and only Ernest et al. (2000) examined both rainfall and plant production. Here, we present a long-term comparative study on rodent abundance and trophic assemblage dynamics in desert grassland and shrubland environments in relation to rainfall and plant production. Examining different but geographically adjacent communities should help us to understand bottom-up controls on different rodent communities across desert landscapes.

The purpose of this study was to compare the importance of rainfall and plant production to the temporal dynamics of adjacent desert grassland and shrubland rodent communities. We addressed the following research questions: Do adjacent grassland and shrubland environments in the same geographic area support similar rodent species, and do both of those species assemblages share similar abundance dynamics over time? Does adjacent grassland and shrubland vegetation production show similar responses to rainfall over time? Do rodent species and trophic groups from adjacent grassland and shrubland environments show similar bottom-up responses to rainfall and plant production over time?

MATERIALS AND METHODS

Study sites.—This research was conducted in the Jornada Basin of the southern Rio Grande Rift valley in the northern Chihuahuan Desert, New Mexico. One study site was in a creosote bush (*Larrea tridentata*) community (shrub site) on a gravelly lower piedmont slope (32°30'N, 106°12'W, 1,327- to 1,351-m elevation), and the other site was in a black grama

(*Bouteloua eriopoda*) grassland (grass site) on a nearby sandy plain (32°35'N, 106°51'W, 1,333- to 1,334-m elevation). A map and photographs of the study sites were presented in Lightfoot et al. (2010). Both study sites were adjacent to National Science Foundation Jornada Basin Long-Term Ecological Research ANPP study plots for creosote bush and black grama grassland communities, where ANPP measurements were taken for this study (Havstad et al. 2006; Huenneke et al. 2001). The creosote bush shrub site was dominated by widely scattered creosote bush shrubs, with the other less-common woody shrubs honey mesquite (*Prosopis glandulosa*) and tarbush (*Flourensia cernua*), perennial bush muhly grass (*Muhlenbergia porteri*), and many species of annual forbs and grasses. The black grama grass site was dominated by the perennial black grama grass, along with other less-common perennial grasses such as spike dropseed (*Sporobolus contractus*) and three-awn (*Aristida purpurea*), widely scattered woody shrubs honey mesquite and broom snakeweed (*Gutierrezia sarothrae*), and many other species of annual and perennial forbs and annual grasses.

Sampling design.—Vegetation and rainfall data were collected over a 12-year period, 1994–2005 (to provide data for 1 year prior to rodent sampling), and rodents were sampled over a 1-year period from 1995 to 2005. Rodent species compositions and densities were sampled in both habitats with circular trapping webs following the protocols of Anderson et al. (1983) and Buckland et al. (1993). Three replicate trapping webs were randomly located in a 1 × 0.5-km area at each study site. Each rodent trapping web was 200 m in diameter (3.1 ha) and contained 12 equally spaced lines radiating from a central point. Each line was 100 m long and had 12 trap stations. The first 4 trap stations were located at 5-m intervals from the center, and the remaining 8 were at 10-m intervals. Rodents were sampled by livetrapping for 3 consecutive nights in both habitats twice each year, in late spring (April–May) and late summer (September–October).

We used 32.5-cm-long Sherman XLKR live traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) appropriate for large rodents such as kangaroo rats and wood rats (Slade et al. 1993). We used rolled oats for bait, placed raw cotton in each trap to reduce physiological stress for the animals, and placed 44-cm lengths of white polyvinyl chloride plastic roofing gutter covers over each trap to protect the traps from sun and rain. Each trapping session lasted for 3 consecutive nights, and consisted of baiting traps in the early evening, then checking the traps early the next morning. Traps were left open during the daytime, and also captured diurnal ground squirrels. All 6 webs were sampled over the same 3-night period, and trapping was conducted only during periods of dry weather. Captured animals were identified to species, and their body mass (live biomass in grams), sex, age class (adult or juvenile), and reproductive status (as reproductively active for conditions; pregnant, vaginal swelling, or lactating, and scrotum enlarged) were recorded. Each animal was temporarily marked with a Sharpie permanent ink marking pen (Newell Rubbermaid, Freeport, Illinois) to determine recapture status over the 3-night

sampling period. All animals were quickly processed and released at the trap location of their capture. Rodents were always trapped during 3 consecutive nights near the new-moon phase, because full or bright moonlight is known to affect desert rodent foraging activity (Price et al. 1984). Animals were treated with care and released unharmed, following guidelines of the American Society of Mammalogists (Sikes et al. 2011), and approved by the University of New Mexico, Animal Care Facility.

Precipitation was measured with Jornada Basin Long-Term Ecological Research rain gauges associated with adjacent (<1 km away) ANPP plots at each study site. Rainfall data were collected monthly at each of the sites from graduated cylinder rain gauges with mineral oil to prevent evaporation. For this study, the monthly rainfall amounts from November to April (1994–2005) were combined to represent the winter rainfall period, and the monthly rainfall amounts from May to October were combined to represent the summer rainfall period. Over the 11-year study period (rodent sampling), these seasonal time intervals resulted in a total of 24 combined monthly seasonal precipitation samples from each of the 2 study sites.

The ANPP was measured from the Jornada Basin Long-Term Ecological Research study plots, and biomass values were calculated from volumetric vegetation measurements as described by Huenneke et al. (2001). Three replicate vegetation measurement plots measuring 70 m on each side were established in each vegetation community type by the Jornada Basin Long-Term Ecological Research program. Each vegetation plot consisted of forty-nine 1-m² permanently marked quadrats. Vegetation was measured from each 1-m² quadrat using the methods of Huenneke et al. (2001), which consisted of volumetric measurements (vertical height and horizontal cover) of foliage canopy by species on each quadrat. Measurements were taken in January, April, and September of each year 1994–2005 to represent seasonal plant growth. This method involved plant species foliage being harvested adjacent to, but not on, the study plots, and harvesting the same range of volumes as measured on the study plots. Harvested plant biomass samples were oven dried, and regression equations of dry weight by volume were developed to relate the harvested plant biomass back to the volumetric values measured on the study plots. This produced plant biomass production, or ANPP (gram/1 m²), estimates for the study plots by plant species, for each season of each year. The plant species were then categorized into functional groups by growth form (grasses, forbs, or shrubs), and by life history (annuals or perennials). ANPP was determined for the winter–spring period (November–April), including perennial plants and spring annual plants, and for the summer period (May–October), including perennial plants and summer annual plants. Over the 11-year study period (rodent sampling), those 2 seasonal measurements per year resulted in a total of 24 samples for ANPP from each of the 2 study sites.

Data analysis.—We originally intended to use the software DISTANCE (Buckland et al. 1993) models to estimate rodent densities, which is why we used the circular trapping webs.

TABLE 1.—Rodent species recorded from the Jornada Basin grass and shrub study sites over an 11-year period, 1995–2005. Taxonomy and trophic group status are based on Findley et al. (1975). Densities (individuals/ha) were averaged over 3 trapping webs per site and all 11 years to provide an index of relative abundance.

Order	Family	Genus	Species	Code	Trophic Group	Grass-site density	Shrub-site density	
Rodentia	Heteromyidae	<i>Chaetodipus</i>	<i>penicillatus</i>	CHPE	Granivore	0.71	0.71	
		<i>Dipodomys</i>	<i>merriami</i>	DIME	Granivore	0.03	7.35	
		<i>Dipodomys</i>	<i>ordii</i>	DIOR	Granivore	8.36	0.09	
		<i>Dipodomys</i>	<i>spectabilis</i>	DISP	Granivore	1.01	<0.01	
		<i>Perognathus</i>	<i>flavus</i>	PEFL	Granivore	0.42	0.31	
	Cricetidae	<i>Neotoma</i>	<i>albigula</i>	NEAL	Folivore	0.34	1.22	
		<i>Neotoma</i>	<i>micropus</i>	NEMI	Folivore	0.41	<0.01	
		<i>Onychomys</i>	<i>arenicola</i>	ONAR	Predator	0.04	0.86	
		<i>Onychomys</i>	<i>leucogaster</i>	ONLE	Predator	0.81	<0.01	
		<i>Peromyscus</i>	<i>eremicus</i>	PEER	Omnivore	0.00	<0.01	
		<i>Peromyscus</i>	<i>leucopus</i>	PELE	Omnivore	0.00	0.42	
		<i>Reithrodontomys</i>	<i>megalotis</i>	REME	Omnivore	0.00	0.19	
		<i>Sigmodon</i>	<i>hispidus</i>	SIHI	Folivore	<0.01	0.32	
		Sciuridae	<i>Spermophilus</i>	<i>spilosoma</i>	SPSP	Omnivore	1.54	0.26

However, we could not use DISTANCE because many of the rodent species were uncommon and numbers of observations were not adequate for estimating densities for those species. For consistent density analyses, we instead chose to use the total number of unique individuals (not recaptures) of each species captured over each 3-day trapping period, averaged over the three 200-m-diameter (3.1-ha) circular webs at each site, to calculate density for each rodent species per 3.1 ha per season. Precipitation, plant, and rodent data were partitioned into 6-month time blocks (November–April and May–October) to accommodate seasonal time-lag analysis sensitive to both spring and summer annual plants. Univariate linear regression and stepwise multiple regression analysis were used to test for relationships between rainfall, ANPP, and rodent densities and biomass over the 11-year period (SAS Institute Inc. 2005).

We partitioned the rainfall and ANPP data into 6-month previous time periods to examine lag-time relationships between plant production and rodents and previous rainfall, and between plant production and rodents at the 2 different sites. All combinations (e.g., 0–6 month/0–6 month, 0–6 month/6–12 month, 0–6 month/12–18 month, 0–6 month/18–24 month, etc.) of rainfall and ANPP from 0- to 6-, 6- to 12-, 12- to 18-, and 18- to 24-month previous time periods were examined to test for lag-time responses in ANPP to rainfall, and rodents to ANPP. Both spring and fall data (6-month intervals) were used separately, not combined for analyses. Over the 11-year study period, 2 seasons of data (spring and fall) each year amounted to a total of 22 time intervals, and 484 combinations, for lag and nonlag (data compared within a time period) response times.

Plant data were analyzed as total ANPP over all species with linear regression analysis, and by plant life forms and life histories with stepwise multiple regression analysis examining the different plant life-form and life-history groups. Rodent data were analyzed separately both as total density and as total biomass over all species with linear regression analysis (too many species [dependent variables] for stepwise regression), and rodent trophic groups were analyzed with stepwise

multiple regression analysis (number of dependent variable groups appropriate).

Normality of data for parametric regression analyses were tested by using the SAS UNIVARIATE procedure (Shapiro–Wilk test [SAS Institute Inc. 2005]). Potential collinearity among predictor variables used in stepwise multiple regression analysis was assessed by performing Pearson correlation analysis and producing cross-correlation matrices for all pairwise combinations of those variables. Comparisons of rodent species composition between the 2 sites was assessed with Srensen’s community similarity index (Krebs 1989) based on species composition distance metrics. Examination of temporal changes in rodent species composition followed the lag-time regression analysis procedure in Collins (2000).

RESULTS

Rodent species assemblages.—We found 11 species of rodents at the grass site and 14 species at the shrub site (Table 1). All 11 species in the grassland also occurred rarely at the shrub site, and 11 of the shrub-site species also were found rarely at the grass site. The numerically dominant and subdominant species differed between the 2 sites, resulting in a Srensen’s similarity index of only 13.8% over the 11-year period. The grass site was numerically dominated by the granivorous Ord’s kangaroo rat (*Dipodomys ordii*) in both numbers of individuals and biomass (Table 1; Figs. 1A and 1C). Other abundant rodent species in the grassland included the diurnal spotted ground squirrel (*Spermophilus spilosoma*), banner-tailed kangaroo rat (*D. spectabilis*), desert pocket mouse (*Chaetodipus penicillatus*), and northern grasshopper mouse (*Onychomys leucogaster* [Table 1; Figs. 1A and 1C]). The spotted ground squirrel, banner-tailed kangaroo rat, Great Plains wood rat (*Neotoma micropus*), and white-throated wood rat (*N. albigula*) represented the primary rodent biomass at the grass site (Table 1; Fig. 1C). The shrub site was dominated by the granivorous Merriam’s kangaroo rat (*D. merriami*) in terms of density and biomass (Figs. 1B and 1D). Other common but

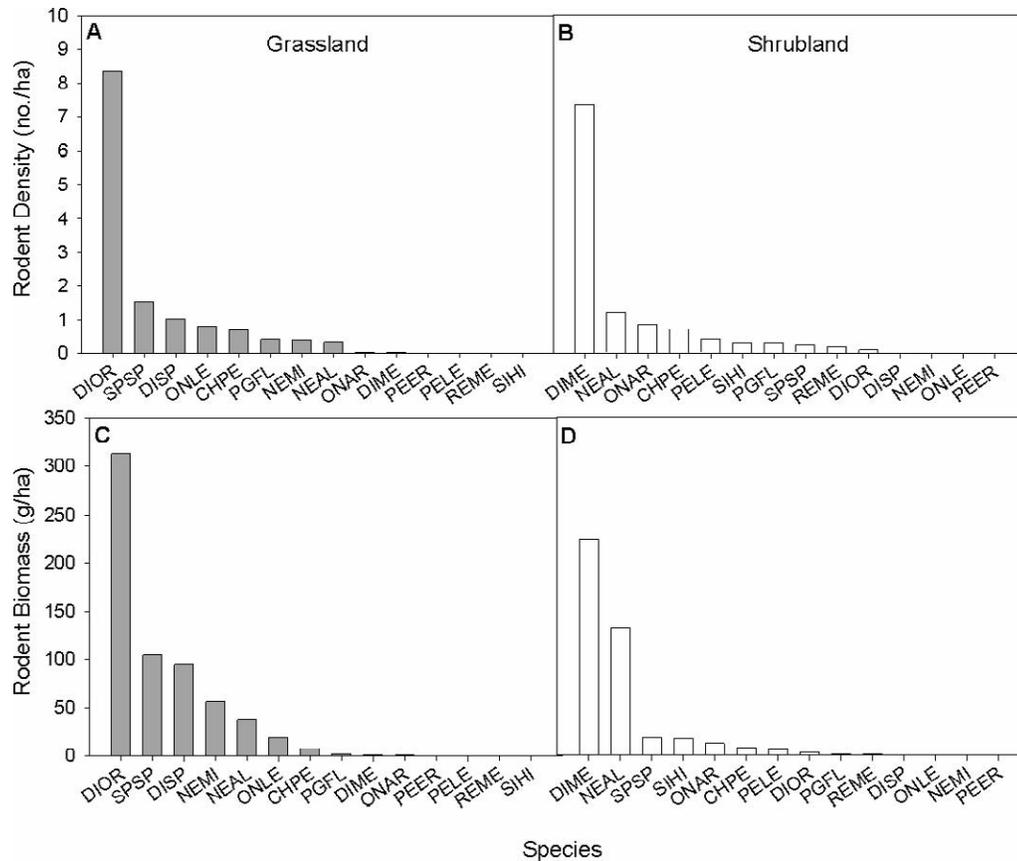


FIG. 1.—Densities of each rodent species from A) the grass site and B) the shrub site, showing the dominance of the kangaroo rats at both sites, DIOR in the grassland and DIME in the shrubland. Live biomass of each rodent species from C) the grass site and D) the shrub site is shown, averaged over 2 seasons per year, from 1995 to 2005. See Table 1 for species name codes.

less abundant species in the shrubland included the white-throated woodrat, Chihuahuan grasshopper mouse (*O. arenicola*), and desert pocket mouse.

Rodent species and trophic composition over time.—Rodent densities and biomass summed over all species in both habitats changed considerably over the course of this study (Figs. 2A, 2B, 2C and 2D). Densities in both habitats peaked at more than 25 individuals/ha at both study sites in 1997 (Figs. 2A and 2B). Summer rainfall, plant production, and rodent densities all gradually increased from summer of 1995 through summer of 1997 (shown as fall amounts in Fig. 2), and all peaked during the year of 1997, coincident with a 1997 El Niño event (Figs. 2E and 2F). Rodent densities at both sites then declined and fluctuated around 10–15 individuals/ha, with a rise again in 2005, coincident with another major El Niño precipitation event. However, rodent densities at the grassland site begin to increase in 1995, peaking in fall of 1997, and declined slowly over a 1-year period, whereas rodent densities at the shrub site increased more slowly, peaking in 1997, and then declined rapidly within 6 months. Plant production at the shrub site peaked in spring of 1998, and examination of data revealed that peak to be the result of a lag response of creosote bush production (not 1998 spring annual plant production) to 1997 rains. Ord's and Merriam's kangaroo rats dominated the rodent communities at the grass and shrub sites, respectively, and

densities of both species increased following rainfall and annual plant production in their respective preferred habitats (Figs. 3A and 3B).

The trophic compositions of the 2 rodent communities were consistently dominated by granivores in terms of density (Table 1; Figs. 2C and 2D). Overall, trophic group density and biomass followed the same general temporal patterns as overall rodent densities and biomass at both sites (Figs. 2C and 2D). Ord's and Merriam's kangaroo rats accounted for most of the granivore densities and biomass at the grass and shrub sites, respectively (Table 1). Omnivores, represented mostly by the spotted ground squirrel, were 2nd in abundance and biomass at the grass site, followed by folivores (wood rats) and predators (northern grasshopper mice). In contrast, at the shrub site, the 2nd most abundant species over time was a folivore (wood rat), whereas omnivores (spotted ground squirrels and white-footed mice [*Peromyscus leucopus*]) were 3rd most abundant (Table 1).

Time-lag analysis (Collins 2000) of rodent species assemblages over time revealed no significant change in the internal composition of the 2 rodent assemblages over the 11-year duration of this study. There were no significant regressions between lag times and rodent species composition over time. Thus, the composition of each rodent community remained relatively constant over the entire 11-year period of this study, despite fluctuations in densities.

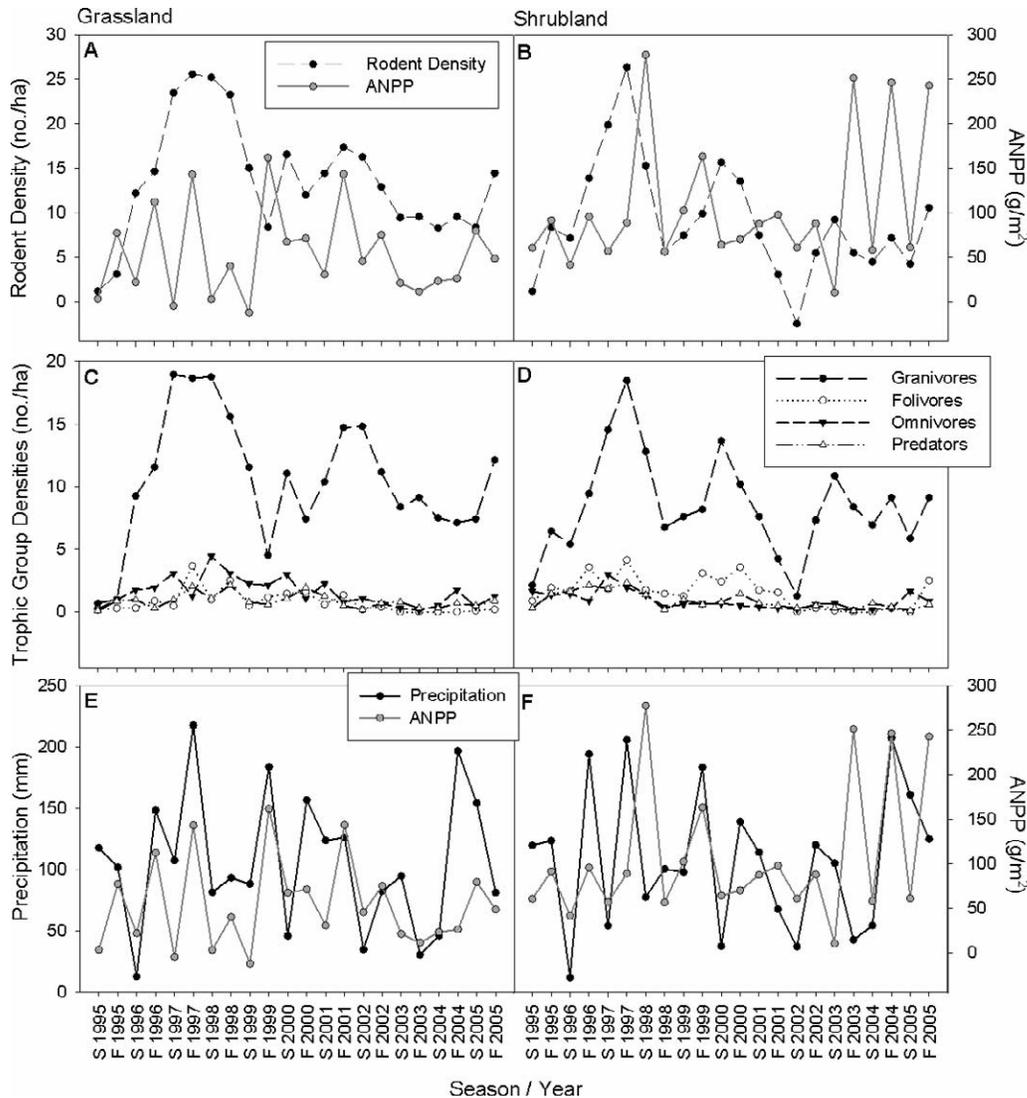


FIG. 2.—Overall rodent density and annual aboveground net primary production (ANPP) A) from the grass site and B) from the shrub site showing the positive response of rodents to ANPP, but a quicker and more prolonged response by grassland rodents to ANPP than by shrubland rodents. Rodent trophic group densities C) from the grass site and D) from the shrub site, showing the dominance of granivores at both sites. Total aboveground plant biomass production and precipitation E) from the grass site and F) from the shrub site, showing the relationship between ANPP and precipitation. See Tables 1S, 2S, and 3S for regression analysis results.

Rainfall, plant production, and rodent production.—Seasonal precipitation and ANPP varied considerably over the study period, but temporal patterns were similar for both study sites (Figs. 2E and 2F), except that ANPP at the shrub site was considerably higher than the grass site during the fall periods of 2003–2005. The years 1997, 2004, and 2005 were El Niño events, with above-average winter precipitation. La Niña events occurred in 1995, 1996, and 2000–2003, with below-average winter precipitation and increasing summer precipitation from fall 1995 through fall 1996, and again in 2004 and 2005. Seasonal rainfall was evenly distributed between summer and winter throughout the study period. However, historically, most of the rain came during the summer season in Jornada Basin (Havstad et al. 2006).

Neither total (all plant species) ANPP or the ANPP of any plant group was significantly predicted by the previous 0–6 months of rainfall at the grass site (Table 1S, DOI 10.1644/11-MAMM-A-391.1S). Total ANPP and annual grass production at the shrub site were not significantly predicted by the previous 0–6 months of rainfall. Total ANPP was significantly predicted by the previous 6–12 months of precipitation at the grass site, and also by perennial grasses alone. At the shrub site, rainfall from the previous 6–12 months also significantly predicted total ANPP, along with ANPP of shrubs alone, and ANPP of perennial forbs alone. Rainfall beyond 1 year did not significantly predict total ANPP or any plant group ANPP at either site. In general, both the grass and shrub sites revealed more significant relationships between rainfall and plant

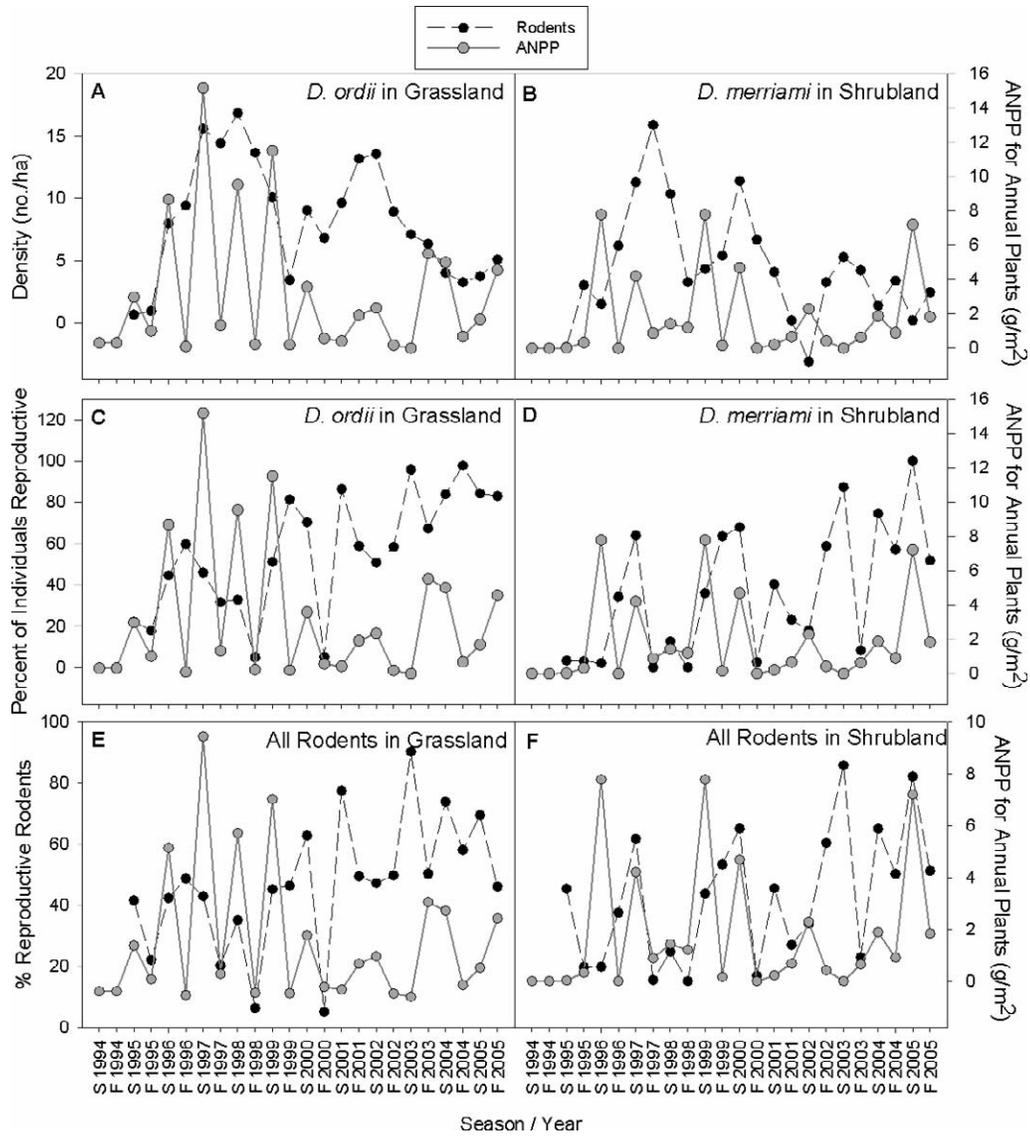


FIG. 3.—A) Density of Ord’s kangaroo rats (*Dipodomys ordii*) and annual forb and grass production from the grass site, B) density of Merriam’s kangaroo rat (*Dipodomys merriami*) and annual forb and grass production from the shrub site, C) percentage of Ord’s kangaroo rats that were reproductively active and annual forb and grass production from the grass site, D) percentage of Merriam’s kangaroo rats that were reproductively active and annual forb and grass production from the shrub site, E) percentage of individuals of all species of rodents that were reproductively active from the grass site, and F) percentage of individuals of all species of rodents that were reproductively active from the shrub site, 1995–2005.

production with a 6-month to 1-year lag response than within a 6-month period.

Rodent density and biomass data for all rodents and rodent trophic groups were normally distributed (Shapiro–Wilk test, $P > 0.05$). Simple linear regression revealed few significant relationships between rainfall and both rodent densities and biomass (Table 2S). Given that there were relatively few and weak cross-correlations (collinearity), we used multiple regression analyses to examine relationships between plant group predictor variables and rodents and rodent trophic groups as response variables.

At the grass site, stepwise multiple regression indicated that variation in the production of cacti, annual grass, and perennial

grass within the current year provided the best model to significantly predict increases in grassland rodent densities and biomass for all rodents combined, and among the various trophic groups (Table 3S). Temporal variation in the density and biomass of all rodent trophic groups except omnivores also was predicted by temporal variation in the production of annual grass and cacti, and mixed results were obtained with perennial grasses and forbs. In general, temporal variation in annual grass production was the best predictor of temporal variation in rodent production at the grass site, especially within the current year, and less so with a 1-year lag response. There were more significant rodent responses to plant production at the grass site within the current year than with a 1-year lag response (Table 3S).

At the shrub site, total rodent density was not predicted by temporal variation in total plant production, but variation in rodent biomass was significantly predicted by variation in annual grass (Table 3S). A 1-year lag-response time did reveal numerous significant relationships between both rodent density and biomass and production of several plant groups, including annual and perennial grass, annual and perennial forbs, cacti, and shrubs at the shrub site (Table 3S). As with findings at the grass site, temporal variation in rodent densities and biomass at the shrub site were best predicted by temporal variation in annual grass production. However, unlike the grass site, there were few significant positive relationships within the current year, and more significant positive relationships between variation in plant and rodent production with a 1- to 2-year lag response (Table 3S).

Rodent reproduction.—The percentage of individual rodents that were reproductively active was higher from the grass site than from the shrub site throughout the 11-year study period (Figs. 3E and 3F). Rodents from the grass site also become reproductively active sooner than those from the shrub site, and the percentage of reproductive rodents tended to increase following El Niño events (Figs. 3E and 3F). Ord's kangaroo rats dominated the grass-site rodent community, and Merriam's kangaroo rat dominated the shrub-site rodent community, and Ord's kangaroo rats had consistently more rapid increases in density and greater densities following increases in rainfall and plant production than did Merriam's kangaroo rats (Figs. 3A and 3B). Reproductive activity of both species followed peaks in the production of annual grasses and forbs (Figs. 3C and 3D), but the timing of reproductive activity was sooner and for a longer duration among Ord's kangaroo rats relative to forb and grass productivity at the grass site than among Merriam's kangaroo rats at the shrub site (Figs. 3C and 3D).

DISCUSSION

Rodent community composition.—Our findings are consistent with known spatial variation in species composition of Chihuahuan Desert rodent communities in relation to dominant vegetation communities (Whitford 1976; Whitford and Steinberger 1989). Ord's and Merriam's kangaroo rats rarely overlap in their habitat distributions (Schroder 1987; Schroder and Rosenzweig 1975; Whitford and Steinberger 1989). Ord's kangaroo rats and other species that dominated the grass site are all known to prefer sandy, desert grassland habitats (Findley et al. 1975). In contrast, Merriam's kangaroo rats and other species that dominated the shrub site are known to prefer gravelly, desert shrub habitats (Findley et al. 1975).

Our findings of relatively stable species compositions of rodent assemblages at both the grass and shrub sites in our study differed from findings of other desert rodent assemblages in the Chihuahuan Desert. At a study site in the northern Chihuahuan Desert near Portal, Arizona, Ernest and Brown (2001) found directional change in the rodent community along with evidence for ecological functional compensation within

rodent guilds over time in relation to temporal shifts in rodent species composition. Thibault et al. (2010) suggested that the 28-year temporal change in the rodent community at the Portal study site was in response to corresponding temporal changes in climate and vegetation at the site. We found no such change in rodent or plant communities over the 11-year period at our Jornada Basin site. In Jornada Basin, vegetation changed significantly over the past century from desertification prior to our study (Schlesinger et al. 1990), but since has remained largely stable (Havstad et al. 2006). Environments and plant communities that are stable over time should support temporally stable rodent assemblages, as we found.

Bottom-up effects on desert rodents.—Our findings are consistent with the general prediction that increased plant production resulting from increased rainfall causes a bottom-up increase in desert rodent densities and biomass, as others have found (Dickman et al. 2010; Kelt 2011; Shenbrot et al. 2010; Thibault et al. 2010). Significant, positive, linear relationships between rainfall and plant production, and plant production and rodent abundance and biomass were similar between the grass and the shrub communities, with plant production, especially of annual grasses, explaining about 20–60% of the variation in rodent abundance over time. Furthermore, El Niño Southern Oscillation events did coincide with large increases in plant production, followed by increases in rodent abundance and biomass.

However, we found few significant direct relationships between rainfall and rodent abundance, indicating that rainfall alone is a poor predictor of bottom-up effects on the desert rodent communities that we studied. Others have found significant relationships between rainfall and rodent abundance (Beatley 1969; Dickman et al. 1999, 2010; Hernández et al. 2005; Kelt 2011; Meserve et al. 2003; Shenbrot et al. 2010), but those studies did not have data for plant production. Perhaps they would have found even stronger evidence for bottom-up effects of rainfall and plant production on rodent abundance if plant biomass data had been available. Rainfall alone does not appear to have any causal mechanism for directly affecting rodent abundance, but rather indirectly by causing plant growth, which does provide direct resources for rodents. Desert plant production provides fresh plant foliage with chemicals such as 6-methoxybenzoxazolinone and high water content that are known to induce and increase rodent reproductive potentials (Shenbrot et al. 2010), and by increasing availability of plant foliage and seeds that are principal food resources to support growth of rodent populations.

Although we did find significant positive relationships between rodent abundance and plant production, the different rodent communities responded in different ways over time. Increases in grassland rodent abundance were predicted by increased annual plant ANPP within a 12-month period of time, whereas rodents at the shrub site did not respond to plant production until 12–24 months after increased plant production. Rodents in the 2 communities responded differently, with the grassland rodents responding more rapidly to annual plant

ANPP, and maintaining relatively high densities for a longer period after peak densities, than did rodents at the shrub site. Rodents from the shrub site not only responded to increased ANPP more slowly, but also declined more rapidly from peak densities, both in 1997–1998 and 2000–2001.

Overall, the positive response of rodents to rainfall and plant production that we found is consistent with other studies showing increases in desert rodents following rainfall elsewhere in the Chihuahuan Desert (Ernest et al. 2000 [in part]; Hernández et al. 2005, 2011; Thibault et al. 2010; Whitford 1976; Whitford and Steinberger 1989), South America (Meserve et al. 2003; Milstead et al. 2007), Australia (Dickman et al. 1999, 2010; Letnic et al. 2011), and Israel (Shenbrot et al. 2010). Ernest et al. (2000) examined rodent response to rainfall and plant production at Sevilleta National Wildlife Refuge in Chihuahuan Desert black grama grassland and creosote bush shrublands similar to those at Jornada Basin, and found that rodent densities increased in both environments over the same period of time, lagging by at least 1 season, approximately 6 months, following rainfall. They did not, however, find a difference in rodent response time to increased plant production between the grass and shrub sites as we did. Creosote bush shrublands at Sevilleta are more transitional and intermixed with grasslands than at Jornada Basin (Lightfoot et al. 2008). The transitional mixing of grassland and shrubland habitats and rodent species may have accounted for the similarity of timing in bottom-up effects of rainfall and plant production on rodent communities at Sevilleta compared to our findings at Jornada Basin.

Granivorous kangaroo rats dominated the rodent communities at both the grass and shrub sites that we studied, and are known to prefer the seeds of annual grasses and forbs (Price 1983; Reichman 1975; Reichman and Van De Graff 1975), which tend to respond fairly quickly to rainfall. Both of our study sites supported a variety of annual grass species such as *Bouteloua barbata*, *B. aristoides*, and *Aristida adscensionis*, the abundance of which was significantly predicted by rainfall within a 6-month period. Price and Joyner (1997) found that annual seed production was the main seed source for heteromyid rodents, not seeds in the soil seed bank, indicating that granivorous kangaroo rats and pocket mice at our sites were responding to recent annual seed production. Kangaroo rats also are known to feed on green foliage in addition to seeds (Kerley et al. 1997; Reichman and Price 1993; Reichman and Van De Graff 1975), and also may have responded to green foliage production, especially at the grassland site. The production of new green vegetation also provides rodents with water and 6-methoxybenzoxazolinone, both of which increase desert rodent reproductive rates (Shenbrot et al. 2010). Because both Ord's and Merriam's kangaroo rats numerically dominated the rodent assemblages at both sites, those 2 species were primarily responsible for the overall positive bottom-up responses of the rodent communities to rainfall and plant production, and to differences in the timing of responses between the grass and shrub sites.

Rodent reproductive potentials.—Individual rodent species also are likely to have different thresholds of response to rain and production based on reproductive potential and differences in food resources, causing bottom-up and top-down controls to vary in importance over time (Brown and Harney 1993; Brown and Zeng 1989). Different reproductive potentials of the dominant rodent species in our study may have accounted for differences in the rodent response to rainfall and plant production between the grassland and shrubland environments. We found that the grassland rodent community, dominated by Ord's kangaroo rat, had consistently higher and more rapid reproductive activity following periods of high rainfall and plant production than did the shrubland rodent community dominated by Merriam's kangaroo rat. Ord's and Merriam's kangaroo rats are known to have different reproductive potentials. Conley et al. (1977) reported from a literature survey that Ord's kangaroo rats produced an average of 3.16 offspring per litter, whereas Merriam's kangaroo rats produced an average of 2.49 offspring per litter. Whitford (1976) working near our study sites, also found that female Ord's kangaroo rats were reproductively active during 2 distinct peak periods per year, in early and late summer months, with a high percentage of females reproductively active, whereas female Merriam's kangaroo rats were reproductively active from February through September, but with less than 10% of females in reproductive condition during the summer months. Whitford and Steinberger (1989) concluded that under favorable conditions, Ord's kangaroo rats had higher natality than did Merriam's kangaroo rats in Jornada Basin. Such differences in reproductive potentials between these 2 dominant species may explain the more rapid density increases of rodents at the grass site we studied, which was dominated by Ord's kangaroo rat, in comparison to the shrub site, which was dominated by Merriam's kangaroo rat.

We present a conceptual model for the differential effects of rainfall on annual and perennial plant production, and consequent plant production effects on Ord's and Merriam's kangaroo rat reproduction over time, given the differential reproductive potentials of the 2 rodent species (Fig. 4). We believe that this conceptual model has application to desert rodent communities worldwide. Different rodent species from different environments should have species-specific temporal variation in reproduction, based on the timing and frequency of breeding individuals, and the number of offspring per pregnancy. For example, Dickman et al. (1999) and Letnic et al. (2011) found different species of Australian desert rodents to have different timing in reproduction following rainfall, and Perrin and Kotler (2005) suggested that differences in reproductive potentials also may be an important mechanism affecting the composition of South African savanna rodent communities. We hope this model prompts researchers to study species-specific rodent reproductive biology and demography as part of an overall understanding of spatial and temporal variation in rodent responses to bottom-up regulation in desert environments.

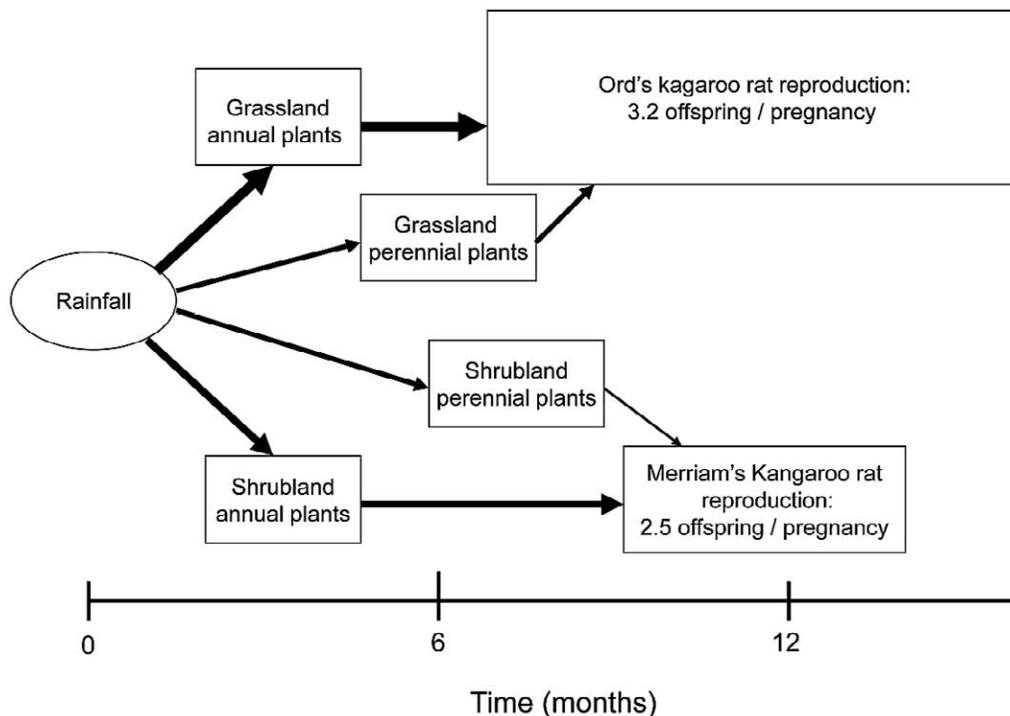


FIG. 4.—Conceptual model for Ord's and Merriam's kangaroo rat responses to bottom-up rainfall and plant production over time, at Jornada Basin grassland and shrubland environments. Rainfall and the production of annual plants triggers reproductive activity, which happens sooner, with more offspring, and over a longer period of time for grassland Ord's kangaroo rats than for shrubland Merriam's kangaroo rats. Rodent reproduction and densities respond less so and secondarily to the production of perennial plants than of annual plants.

ACKNOWLEDGMENTS

Funding for this research was provided by the National Science Foundation, grant DEB 9527083 for this project and grant DEB 0080412 to the Jornada Basin Long-Term Ecological Research program. We thank the Jornada Basin Long-Term Ecological Research field crew members, especially C. McGlone and S. Richmond, who helped collect the data for this research. J. Anderson, Jornada Basin Long-Term Ecological Research Program Manager, also assisted with all aspects of this research.

SUPPORTING INFORMATION

Table S1. Results of univariate linear regression analysis between rainfall and plant production over the 11-year study. Table S2. Results of univariate linear regression analysis between rodent densities and biomass, and rainfall over the 11-year study. Table S3. Results of multiple step-wise multiple regression analysis between rodent densities and biomass, and plant production over the 11-year study. Fig. S1 A) Overall rodent live-weight biomass and annual net primary production (ANPP) from the grassland and B) shrubland sites; C) rodent trophic group biomass from the grassland and D) shrubland. DOI: 10.1644/11-MAMM-A-391.1S

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Submitted 20 November 2011. Accepted 5 March 2012.

Associate Editor was Harald Beck.