Long-term insights into the influence of precipitation on community dynamics in desert rodents

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Arid systems are characterized by spatiotemporal variability in resources and, as such, make ideal systems for examining the role of resource limitation in the long-term dynamics of populations. Using 28 years of data, we examine the long-term relationships of 3 guilds of desert rodent consumers with precipitation and primary productivity in a changing environment. Lags in rodent response to precipitation increased with increasing trophic level over the entire time series, consistent with resource limitation. However, we found that consumer–resource dynamics are complex and variable through time. Precipitation exhibited increasing influence on both primary producers and consumers in this system over time. Experimental evidence suggests that reorganization of community composition, coincident with environmental change, likely explains some of the increasing influence of precipitation. Additional, indirect evidence suggests some role for increasing shrub density and changing precipitation regimes. Results from our long-term study demonstrate that the global phenomena of changing precipitation regimes, increasing frequency of extreme climatic events, and shrub encroachment are likely to have strong, interactive impacts in reorganizing ecological communities, with significant consequences for ecosystem dynamics. DOI: 10.1644/09-MAMM-S-142.1.

Key words: consumer dynamics, desertification, desert rodents, guild, precipitation, resource limitation, resource pulses, shrub encroachment, temporal dynamics

Resource pulses and resource variability can play important roles in the dynamics of populations, communities, and ecosystems (Anderson et al. 2008; Chesson et al. 2004; Drever et al. 2009; Noy-Meir 1973; Polis 1991; Stapp and Polis 2003; Yang et al. 2008). In particular, recent studies have shown that resource variability can influence population dynamics, species coexistence, and bottom-up and top-down regulation of trophic levels (Chase et al. 2000; Chesson et al. 2004; Lima et al. 2006; Yang 2008). Because arid systems are characterized by heterogeneity in resource availability through space and time, driven primarily by pulses of precipitation and nutrient availability (Collins et al. 2008; Garcia-Moya and McKell 1970; Guo and Brown 1997; Noy-Meir 1973; Polis 1991; Rosenzweig 1968), arid systems are ideal systems in which to examine whether and how resource variability dictates the long-term dynamics of populations. Much of pulse-reserve theory has been developed using the response of desert plants to precipitation as a model system (Anderson et al. 2008; Chesson et al. 2004; Noy-Meir 1973; Schwinning and Sala 2004). Although the positive relationship between precipitation and primary productivity in arid systems is well documented, the consequences of this relationship for consumer–resource dynamics in a diversity of communities remain unclear. Understanding this relationship is critical to understanding disease outbreaks (Enscore et al. 2002), impacts of global climate change across ecosystems (Easterling et al. 2000), and desertification (Van Auken 2000).

The dynamics of small mammals in arid systems have been studied intensively because they are model organisms in population ecology and often serve as vectors or reservoirs for zoonotic diseases (Lima et al. 2003; Ostfeld and Holt 2004; Stenseth 1999; Yates et al. 2002). Numerous studies have documented the influence of precipitation or primary productivity, or both, on rodent populations across both large and small spatial and temporal scales. At large spatial scales species richness and abundance of small mammals typically

are correlated with mean annual precipitation (Brown 1973, 1975; Brown and Ernest 2002; Brown and Harney 1993; Shenbrot et al. 1994). However, predation risk can interact with these processes to yield significant differences in abundances of small mammals under similar precipitation regimes (Kotler 1984; Kotler and Brown 1988; Rosenzweig and Winakur 1969). At local scales increases in small mammal abundance following precipitation events have been documented repeatedly (Beatley 1969; Brown 1973; Chew and Butterworth 1964; Ernest et al. 2000; Hafner 1977; Jaksic et al. 1997; Letnic et al. 2005; Lima et al. 1999, 2002; Meserve et al. 1995, 2003; Orland and Kelt 2007; Stapp and Polis 2003; Whitford 1976; Yates et al. 2002). However, such positive responses do not always occur (Brady and Slade 2004; Ernest et al. 2000; Gillespie et al. 2008; Meserve et al. 2003; Reynolds 1958), and, in some cases, extreme precipitation events can actually cause populations to decline (Fitch 1948; Grinnell 1939; Kelt et al. 2008; Reynolds 1958; Thibault and Brown 2008; Valone et al. 1995).

Long-term studies provide opportunities for elucidating mechanisms underlying this apparent inconsistency, because they provide data spanning the range of variation individual sites experience through ecological time. Since 1977 a community of desert rodents near Portal, Arizona, has been sampled monthly on both control plots and on plots from which the dominant consumers (kangaroo rats [*Dipodomys merriami*, *D. ordii*, and *D. spectabilis*]) have been removed experimentally. During this period density of shrubs across the entire site has increased by a factor of at least 3 (Brown et al. 1997), driving significant changes in species composition (Ernest et al. 2008; Thibault et al. 2004). Several studies of the dynamics between precipitation and rodent populations have been done at this site. Early analyses revealed peaks in abundance that corresponded to 3 seasons of high winter precipitation in the 1980s that were related to El Niño Southern Oscillation events (Brown and Heske 1990), but the intense rains associated with a 1983 tropical storm contributed to the local extinction of the formerly dominant banner-tailed kangaroo rat (*D. spectabilis*—Valone et al. 1995). In 2000, analysis of the relationships among precipitation, annual plant abundance, and rodent abundance revealed significant, positive relationships between precipitation and annual plant abundance—the primary resource base—but not rodent abundance (Ernest et al. 2000). The complexity and nonlinearity of the dynamics operating within this community were further supported by the catastrophic mortality of kangaroo rats following a 1999 flood (Thibault and Brown 2008) and rigorous analysis of population dynamics of kangaroo rats at the site (Lima et al. 2008). Taken together, this suite of studies implies that the very nature of consumer–resource dynamics could be changing over time at this site.

A number of reasons could account for why the whole-community abundance of rodents shows a complex and dynamic relationship with precipitation. In addition to the nonlinearities associated with extreme climatic events such as drought and floods, the changing composition of the rodent community has likely affected the consumer–resource dynamics at Portal through a number of pathways. The change in species composition resulting from a decline in kangaroo rats and an increase in pocket mice (*Chaetodipus baileyi* and *C. penicillatus*—Thibault et al. 2004) could impact community-level responses to precipitation if these genera respond differently to precipitation. The shift from larger kangaroo rats to smaller pocket mice also could affect the relationship between rodents and precipitation indirectly through other mechanisms. Previous work at the site showed that the increasing dominance of pocket mice resulted in a doubling of the total rodent abundance, because more small individuals can be supported on the same amount of resource (White et al. 2004). This long-term increase in abundance could obfuscate the relationship with precipitation by changing the number of individuals a given amount of precipitation will support. Many of these changes in the rodent community were driven by the shift in habitat from desertified grassland to a Chihuahuan Desert shrubland (Brown et al. 1997). This shift in habitat favored shrub-affiliated species of rodents at the expense of grass-affiliated species (Ernest et al. 2008) and also could have affected the temporal relationships between precipitation, plant production, and rodent response. Finally, previous efforts examined community dynamics across all trophic guilds, ignoring potential differences in the consumer–resource dynamics among granivores, folivores, and insectivores. Given all the documented changes at the site and known differences in natural history among species (Hoffmeister 1986), any or all of these observed shifts—compositional change, long-term abundance trajectories, differences in trophic guilds, and vegetation changes—could result in complex dynamics between precipitation and the rodent community.

Using the experimental manipulations of rodent community composition, an additional 11 years of data since the analyses of Ernest et al. (2000), and more advanced statistical methods than used in either Ernest et al. (2000) or Brown and Ernest (2002), we ask the following questions: What are the long-term relationships between precipitation, annual plant abundance, and abundance and energy use within rodent trophic guilds?; Have consumer–resource dynamics changed against the backdrop of compositional change in response to desertification?; and How does the experimental exclusion of all resident species of *Dipodomys* change consumer–resource dynamics?

MATERIALS AND METHODS

Study site.—We used data from a long-term study established in 1977 by J. H. Brown and colleagues and located at the edge of the Chihuahuan Desert, in the foothills of the Chiricahua Mountains (elevation 1,330 m, 6.5 km east and 2 km north of Portal, Cochise County, Arizona). Annual precipitation in the region is distributed bimodally, with approximately 60% of the annual rainfall falling in the summer and the remaining 40% in the winter (Brown and

TABLE 1.—Delineation of trophic guilds at the study site near Portal, Arizona.

Guild	Genus	Species
Granivores	*Baiomys*	*B. taylori*
	Chaetodipus	*C. baileyi, C. hispidus, C. intermedius, C. penicillatus*
	Dipodomys	*D. merriami, D. ordii, D. spectabilis*
	Perognathus	*P. flavus*
	Peromyscus	*P. eremicus, P. leucopus, P. maniculatus*
	Reithrodontomys	*R. fulvescens, R. megalotis, R. montanus*
Folivores	*Neotoma*	*N. albigula*
	Sigmodon	*S. fulviventer, S. hispidus, S. ochrognathus*
Insectivores	*Onychomys*	*O. leucogaster, O. torridus*

Ernest 2002). A weather station has collected meteorological data at the site continuously since 1980. The 20-ha site was fenced to exclude cattle and consisted of 24 experimental plots, each 0.25 ha in size. Plots were constructed using hardware-cloth fencing—total aboveground (60 cm) + belowground (30 cm) height = 90 cm—to inhibit rodents digging under the fence; aluminum flashing was secured to the top edge of the fencing to deter climbing rodents. Three rodent treatments were randomly distributed among the 24 plots: controls ($n = 10$) that allow equal access to all rodents via large holes in the fence at ground level, plots from which all species of *Dipodomys* (*D. merriami*, *D. ordii*, and *D. spectabilis*) were removed (1977–1987: $n = 4$; 1988–present: $n = 8$) and that have holes that are smaller than a kangaroo rat's skull, and plots from which all rodents were removed (i.e., total rodent exclosures, $n = 6$) that have no holes. We used data from only the control and *Dipodomys* removal plots in these analyses.

On each plot rodents were surveyed monthly since 1977, over a period of 2 or 3 nights during the new moon phase, using Sherman traps (7.6 × 8.9 × 22.9 cm, model LFA; H. B. Sherman Traps, Tallahassee, Florida) baited with millet. Traps were placed at each of 49 permanently staked locations (7 × 7 grid, with 6.25 m between stakes) per plot for 1 night. Captured rodents were measured, weighed, identified to species and sex, and uniquely marked with a passive integrated transponder tag (Biomark, Boise, Idaho) or ear tag (National Band and Tag Co., Newport, Kentucky), and their reproductive condition was determined. Our livetrapping methodology followed guidelines of the American Society of Mammalogists (Gannon et al. 2007) and has been approved repeatedly by various animal care and use committees (most recently at Utah State University).

Annual plants and perennial grasses (collectively referred to herein as annuals) have been surveyed biannually in a consistent manner since 1988. Surveys of the plants occur after the winter (March–April) and summer (August–September) growing seasons. Each plot has 16 permanent, staked quadrats, each 0.5 m^2 in area, within which each live stem is identified to species. A thorough treatment of the site and methods can be found in Brown (1998).

Data analysis.—Given the bimodality of the precipitation regime at the site and corresponding plant censuses, all data were analyzed seasonally, as in Ernest et al. (2000). Precipitation was summed for each precipitation season, summer (April–September) and winter (October–March). Each rodent species that was captured at the site was assigned to 1 of 3 foraging guilds (Table 1), as in Goheen et al. (2005).

Within each guild rodent data were aggregated to correspond to the 2 distinct pulses of annual plants and to avoid complications arising from the tendency of some rodent species to reduce activity in winter (e.g., *C. penicillatus*—Mantooth and Best 2005). Rodent abundances represent total numbers of captures, and energy use was calculated by summing the energy use of all individuals estimated from the allometry for field metabolic rates: energy use = 5.69 × mass$^{0.75}$; $r^2 = 0.99$ (data from Nagy et al. 1999; see White et al. 2004 for details). For each treatment and monthly census period abundance and energy use were summed across plots. Three-month averages of these values were taken, 2 per year corresponding to winter (April–June) and summer (September–November) crops of annual plants.

For each season and each treatment (controls and removals) we had data on total precipitation, total annual plant stem counts, and total abundance and energy use of granivorous, folivorous, and insectivorous rodents. The influence of precipitation on each of these trophic levels was evaluated separately using generalized linear models to explain variation in abundance or energy use as a function of variation in precipitation. We constructed models that had a 1st-order autoregressive error structure to account for autocorrelation within the time series (Fox 2002; White and Gilchrist 2007). To investigate lagged responses we included same-season precipitation (Ppt_t) and precipitation from the previous season (Ppt_{t-1}) and 2 seasons prior (Ppt_{t-2}). We also ran parametric multiple linear regression analyses, and because the results were qualitatively similar to those of the generalized linear models, we report these R^2 values for comparative purposes.

These analyses were performed for the entire time series (1980–2007 for the rodents, 1988–2008 for the plants) and then for each of 3 distinct time periods based on variation in rodent community composition: time period 1 (1980–1987, before local extinction of the dominant kangaroo rat *D. spectabilis*), time period 2 (1988–1995, decline to local extinction of *D. spectabilis*, but prior to colonization of *C. baileyi*), and time period 3 (1995–2008, after colonization by
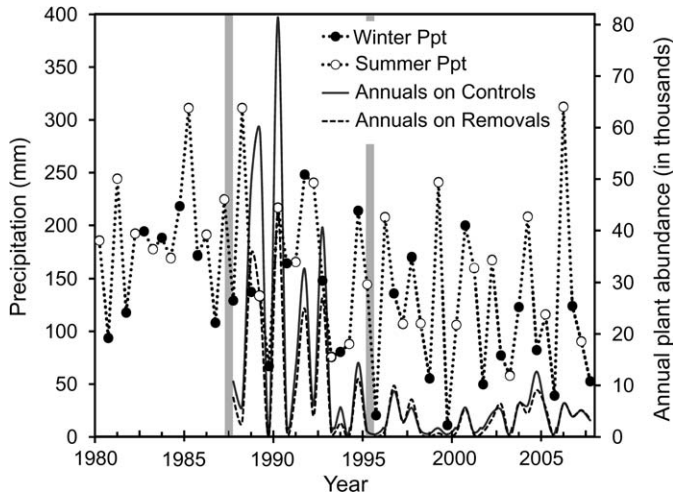
Fig. 1.—Temporal trends in seasonal precipitation and annual plant abundances across treatments on control plots and *Dipodomys* removal plots at a study site near Portal, Arizona, 1980–2008. Vertical gray lines delineate time periods of analysis; annuals refer to annual plants (see text). Precipitation has generally been decreasing over time, but a record amount of precipitation fell in summer 2006.

C. baileyi). Analyses are limited in time period 1 because we had only 4 (rather than 8) removal plots and complete plant census data are not available. Plant abundance data deviated markedly and significantly from normal ($P < 0.001$) and were log-transformed, which yielded data that were normally distributed, prior to analysis. All analyses were performed in R (http://www.r-project.org), using the car and nlme libraries as described in Fox (2002). We used an α of 0.10 for these analyses rather than the traditional 0.05, because we are interested in biologically meaningful influences of precipitation on observed dynamics. Although relationships characterized by $0.05 < P \leq 0.10$ are relatively weak, we believe that they are still biologically meaningful.

RESULTS

Annual plants and precipitation.—Seasonal precipitation varied dramatically through time at Portal, ranging from a low of 10.9 mm in the winter of 2000 to a high of 312.3 mm in the summer of 2006 ($\overline{X} = 149.4$ mm ± 72.3 *SD*; Fig. 1). Similarly, annual plant abundance fluctuated markedly over time on both the control and removal plots, with several seasons yielding no plants and some years >30,000 stems (controls: $\overline{X} = 10,088$ stems $\pm 17,502$ *SD*; removals: $\overline{X} = 6,511 \pm 10,058$ stems; Fig. 1). These extremely high abundances were composed overwhelmingly of needle grama grass (*Bouteloua aristidoides*) and occurred toward the beginning of the study when grass was much more abundant and shrub densities were lower than at present (Brown et al. 1997). Temporal trends in annual plant abundance were nearly identical across treatments (Fig. 1), and both were significantly influenced by precipitation in the same season (Table 2). Although it is clear that low levels of precipitation yield few plants, much greater variability in the relationships

exists when precipitation is high, as reflected in the relatively low R^2 values (<0.4; Table 2). Similar results are found within time periods 2 and 3 (Table 2), although the effect of same-season precipitation in time period 2 is weaker ($P = 0.10$–0.12).

Rodent guilds and precipitation, 1980–2007.—The long-term, increasing trend in abundance discussed above is apparent in Fig. 2 for the granivores and the insectivores (generalized linear model on controls, $P = 0.001$ and 0.069, respectively) but not for the folivores ($P = 0.585$). In contrast, energy use for all groups has consistently failed to show a directional trend over time (generalized linear model on controls, $P = 0.145$ for granivores, 0.121 for insectivores, and 0.960 for folivores; Fig. 2).

Strong community responses to precipitation can be seen in the responses in both abundance and energy use of all guilds to the high precipitation received in the summer of 2006 (Figs. 1 and 2), although 2 previous summers at the site received similar quantities of precipitation to which the rodent community did not respond as markedly (Figs. 1 and 2). Over the course of the entire study, precipitation is an important predictor for both abundance and energy use of all 3 guilds on the control plots, although its explanatory power is low (Fig. 2; Tables 2 and 3). Although the plants responded to same-season precipitation, granivores and folivores showed significant responses to precipitation in the previous season (Ppt_{t-1}), and insectivores did not respond until 2 seasons later (Ppt_{t-2})—that is, a full year later (Tables 2 and 3). On the removals, in the absence of kangaroo rats, responses were comparable, except that insectivores failed to show any significant relationship to precipitation, and granivores showed weak relationships to Ppt_{t-2} (Fig. 2; Tables 2 and 3). Across all of these models abundance and energy yielded similar results (as indicated by values of R^2 and P) despite the marked differences in their long-term temporal trends (Fig. 2; White et al. 2004).

Rodent guilds and precipitation across time periods.—The effect of precipitation on abundance and energy use of rodents at Portal varied both through time and across treatments (Fig. 3). Time period 1 (1980–1987) is characterized by virtually no significant effects on any guild located on either treatment (Fig. 3; Tables 2 and 3). The only exception occurs for granivores on removal plots, for which both abundance and energy use are significantly, but negatively, related to Ppt_{t-2} (Tables 2 and 3). During this time, however, granivores were very rare on the few removal plots, with average abundances ranging between 5.0 and 18.7 individuals (Fig. 2).

In time period 2 rodent abundance and energy use reached their minima (Fig. 2), coincident with 3 consecutive seasons of precipitation below 90 mm (Fig. 1), and 1 species (*D. merriami*) accounted for approximately 80% of the rodent energy use (Thibault and Brown 2008). However, analyses reveal a significant influence of precipitation across guilds on only the removal plots during this time. Granivores and folivores on removal plots responded to Ppt_{t-1}, as they did over the whole time series (Fig. 3; Tables 2 and 3).

TABLE 2.—Relation of abundance of annual plants and 3 foraging guilds of rodents to precipitation, as shown by parameters of generalized linear models, over the course of the study and for the 3 time periods (1980–1987, 1988–1995, and 1995–2008 for plants, and 1995–2007 for rodents; see text), incorporating time lags. Time lags for precipitation (Ppt) are the same season (t), the previous season (t−1), and 2 seasons prior (t−2; see text). AP indicates autoregressive parameter for the models. Only results representing significant ($P \leq 0.10$) effects of precipitation on at least 1 of the treatments for a particular taxon and time combination are presented.

| Time period | d.f. | Ppt time lag | Controls | | | | | | Removals | | | | | |
			Parameter estimate	SE	t	P	AP	R^2	Parameter estimate	SE	t	P	AP	R^2
Annual plants														
1988–2008	41	t	0.02	0.00	4.58	0.00	0.11	0.38	0.01	0.00	4.30	0.00	0.15	0.36
1		No data available												
2	15	t	0.00	0.00	1.66	0.12	0.71	0.37	0.00	0.00	1.80	0.10	0.68	0.34
3	26	t	0.01	0.00	3.21	0.00	0.01	0.34	0.01	0.00	3.22	0.00	0.07	0.33
Granivores														
1980–2007	53	t−1	0.15	0.05	2.74	0.01	0.80	0.11	0.14	0.05	3.04	0.00	0.88	0.16
1	13	t−2	−0.06	0.09	−0.68	0.51	0.10	0.07	−0.05	0.02	−2.09	0.07	0.34	0.41
2	15	t−1	0.01	0.03	0.47	0.65	0.67	0.17	0.05	0.02	2.03	0.07	0.22	0.33
3	25	t−1	0.31	0.10	3.00	0.01	0.46	0.38	0.26	0.10	2.72	0.01	0.55	0.32
		t−2	0.15	0.09	1.61	0.12			0.14	0.08	1.72	0.10		
Insectivores														
1980–2007	53	t−2	0.03	0.01	2.60	0.01	0.38	0.08	0.01	0.01	1.03	0.31	0.17	0.06
1	13	No significant results												
2	15	t−2	0.03	0.01	3.38	0.01	0.39	0.44	0.01	0.01	1.38	0.19	0.34	0.41
3	25	t−2	0.06	0.03	2.22	0.04	0.22	0.19	0.03	0.01	2.21	0.04	0.17	0.22
Folivores														
1980–2007	53	t−1	0.02	0.01	2.66	0.01	0.60	0.13	0.02	0.01	3.26	0.00	0.88	0.16
1	13	No significant results												
2	15	t−1	0.01	0.01	1.37	0.20	0.56	0.22	0.01	0.01	2.37	0.04	0.53	0.44
3	25	t−1	0.03	0.01	2.29	0.03	0.54	0.32	0.03	0.01	2.34	0.03	0.56	0.34

Abundance and energy use of insectivores on removal plots were significantly influenced by precipitation in the same season (Fig. 3; Tables 2 and 3). Insectivores also showed the only significant relationship found on the control plots, responding to Ppt_{t-2}, as over the whole time series (Fig. 3; Tables 2 and 3).

The dynamics appear to change more markedly in time period 3, after colonization of the site by *C. baileyi* in 1995. The effect of precipitation was much greater across guilds at that time than in previous periods, and dynamics on the 2 treatments converge (Fig. 3; Tables 2 and 3). The same significant relationships with precipitation that were found for the whole time series were seen for this time period, with similar results seen across treatments and for both abundance and energy use (Fig. 3; Tables 2 and 3). In addition, abundance and energy use of granivores show weak responses to Ppt_{t-2}, as exemplified by the maintenance of high abundances for 2 seasons after the record rainfall of summer 2006.

DISCUSSION

Overall, the results support the idea that precipitation plays a key role in the dynamics of the rodent community at Portal. In contrast to previous studies that examined the rodent community as a whole, here we detected a weak, but

significant, positive relationship between precipitation and rodent responses across the entire time series when the community was divided into trophic guilds. Time lags in response to precipitation increased with increasing trophic level. Folivores and granivores responded to precipitation of the previous season, whereas insectivores responded to precipitation from the previous year. The short lag from precipitation to folivore and granivore response is consistent with the dependence of these trophic groups on annual plants (a major food resource in this system). The increased lag for insectivores presumably results from the lag for primary consumers, such as grasshoppers, to convert primary productivity into increased biomass, and that the insects are primarily available only during the warm months of the year, whereas seeds and leaves remain available for longer periods in the winter months. Studies from other systems typically have reported similarly lagged responses (Previtali et al. 2009; Stapp and Polis 2003; Yates et al. 2002), further supporting the role of precipitation in consumer–resource dynamics.

Although our results illustrate how precipitation drives numerical and compositional changes within desert rodent communities, they also indicate that this relationship is complex and temporally dynamic. Although statistically significant, the amount of variance in rodent abundance explained by precipitation was low (all $R^2 < 0.2$) when the whole time series is considered. When the analyses were
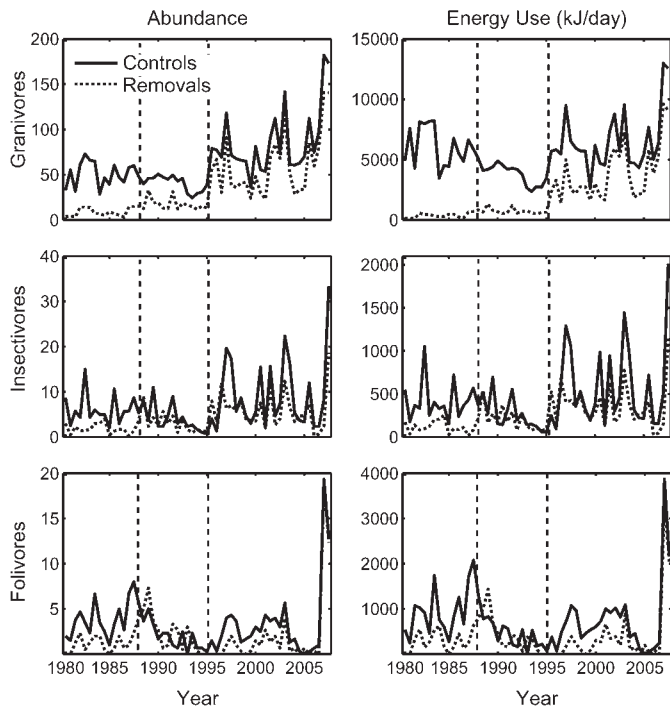
FIG. 2.—Temporal trends in abundance and energy use of 3 guilds of rodents across treatments at the Portal, Arizona, long-term research site. Energy use is based on allometry of field metabolic rates. Treatments are control plots (solid lines) and *Dipodomys* removal plots (dotted lines). Three-month seasonal averages are presented (see text). Differences between treatments and through time are driven in part by the differential number of plots included (see ''Materials and Methods'' for details). Vertical lines delineate the 3 time periods of analysis.

restricted to only time period 3, the general pattern of relationships between precipitation and rodent populations was the same, but the relationships were substantially stronger. Coupled with the lack of significant effects found in previous studies encompassing shorter time series (Ernest et al. 2000), these results suggest that long-term relationships might not reflect long-term processes but might instead be driven by the strong, positive relationships in time period 3. Moreover, the strength of these relationships is due in large part to the dramatic impact of the extreme precipitation received in the summer of 2006 (Fig. 4), further supporting the conclusion that the long-term results do not reflect processes that have been consistently operating at the site. So, why does precipitation appear to exert greater influence on the dynamics in time period 3? Our results provide some empirical support for 3 factors that could have altered the relationship between precipitation events and rodent population dynamics: shifts in species composition; underlying changes in vegetation; and shifts in the timing and distribution of precipitation events.

The effects of changing species composition.—One possible explanation for the changing relationship between precipitation and rodent dynamics lies in the changing species composition of the rodent community. As the community shifted from dominance by large-bodied kangaroo rats to smaller pocket mice, the relationships between precipitation and rodent community metrics (i.e., abundance and energy use) became stronger. For the granivorous rodents these changes could be related to one another. Reynolds (1958) found that abundance of *D. merriami* was not correlated with precipitation or grass production (but see Lima et al. 2008). Given the territorial behavior of kangaroo rats (Randall 1984), it is possible that during the first 2 time periods granivorous rodents also were limited by the availability of space, which dampened fluctuations in response to resource availability.

TABLE 3.—Relation of energy use of 3 foraging guilds of rodents to precipitation, as shown by parameters of generalized linear models. Time periods, time lags for precipitation, definition of AP, and significance of results are as in Table 2.

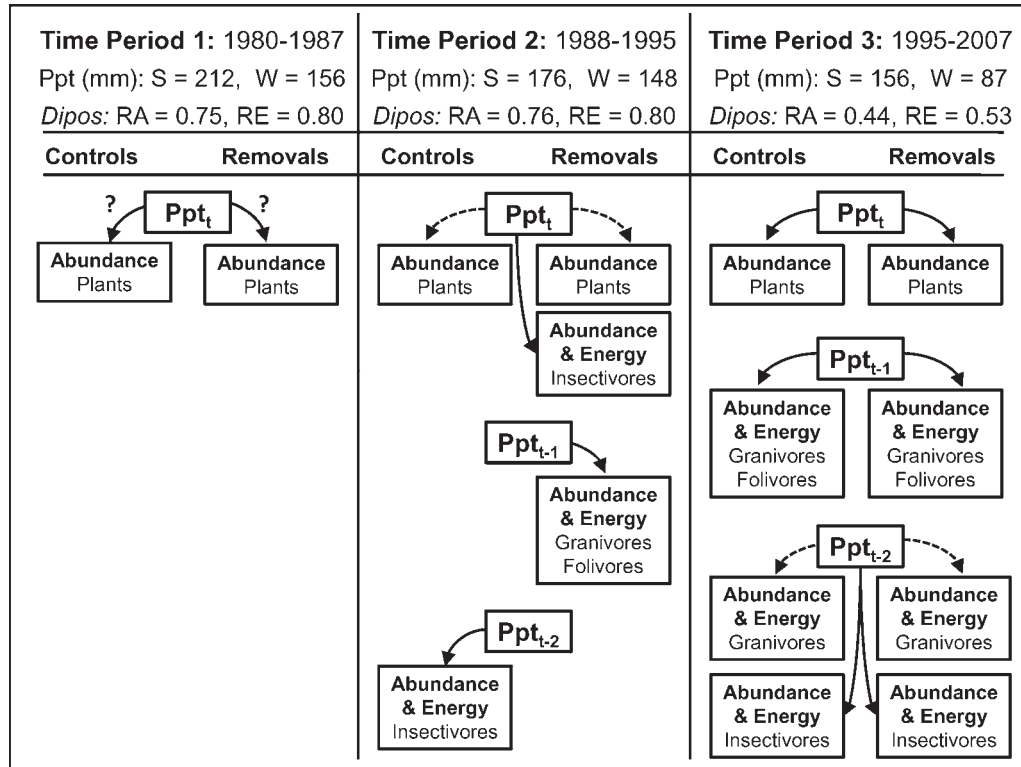| Time period	d.f.	Ppt time lag	Controls Parameter estimate	SE	t	P	AP	R^2	Removals Parameter estimate	SE	t	P	AP	R^2
Granivores														
1980–2007	53	t−1	10.46	3.90	2.68	0.01	0.7	0.1	8.69	2.69	3.23	0.00	0.92	0.15
		t−2	2.14	3.37	0.63	0.53			3.82	2.29	1.67	0.10		
1	13	t−2	−8.55	9.59	−0.89	0.40	0.28	0.17	−2.07	0.90	−2.29	0.05	0.49	0.28
2	15	t−1	−1.09	2.13	−0.51	0.62	0.85	0.13	2.00	0.74	2.70	0.02	0.06	0.42
3	25	t−1	23.60	6.93	3.41	0.00	0.40	0.46	16.72	5.94	2.81	0.01	0.67	0.28
		t−2	12.39	6.06	2.05	0.05			9.64	5.12	1.88	0.07		
Insectivores														
1980–2007	53	t−2	1.76	0.72	2.43	0.02	0.34	0.07	0.43	0.41	1.05	0.30	0.19	0.06
1	13	No significant results												
2	15	t−2	1.83	0.56	3.26	0.01	0.46	0.40	0.59	0.38	1.55	0.15	0.33	0.46
3	25	t−2	3.20	1.56	2.05	0.05	0.21	0.17	1.73	0.80	2.15	0.04	0.18	0.21
Folivores														
1980–2007	53	t−1	2.94	1.27	2.32	0.02	0.47	0.11	3.26	1.01	3.24	0.00	0.59	0.17
1	13	No significant results												
2	15	t−1	1.25	1.36	0.92	0.38	0.69	0.34	2.29	1.05	2.18	0.05	0.44	0.13
3	25	t−1	6.15	2.59	2.38	0.03	0.36	0.30	5.23	2.26	2.31	0.03	0.52	0.32

FIG. 3.—Summary of seasonal precipitation, kangaroo rat (*Dipodomys*) dominance, and the significant relationships detected between precipitation and annual plant abundance and guild-specific rodent abundance and energy use in control plots and plots with kangaroo rats removed in Portal, Arizona, for 3 time periods. Solid arrows indicate significant (i.e., $P < 0.05$) relationships, whereas dashed lines signify $0.05 < P \leq 0.10$. Abbreviations: Ppt = precipitation (seasonal mean); S = summer; W = winter; Ppt_t = precipitation in same season; Ppt_{t-1} = precipitation in previous season; Ppt_{t-2} = precipitation 2 seasons prior; *Dipos* = *Dipodomys* spp.; RA = relative abundance; RE = relative energy use (both as mean proportions of community totals). Reliable data on plant abundances in time period 1 were not available. The effects of precipitation increase over time, coincident with decreasing kangaroo rat dominance and precipitation.

This assumes that individual home-range size does not change with resource availability on the short timescale at which we conducted these analyses. Orland and Kelt (2007) proposed a similar mechanism to account for the lack of density increases in adult pocket mice following food addition experiments in an arid system in California. This mechanism may operate even more strongly in communities dominated by kangaroo rats, and consequently the role of space as a limiting resource should decrease with declining kangaroo rat populations,

FIG. 4.—Photographs from the study site before (2005, on left) and after (2006, on right) record precipitation in 2006, showing difference in plant cover. The photographs are of different plots, approximately 400 m apart, but the fence line apparent in each serves as a point of comparison and scale. Photo credit: Alan Ernest.

potentially leading to the shift in observed correlations between the rodent community and precipitation.

The temporal dynamics on the *Dipodomys* removal plots provide further, albeit limited, support for the role of kangaroo rats in the changing influence of precipitation. In time period 2 precipitation significantly influenced abundance and energy use of all 3 rodent guilds on the removal plots but not on the control plots. On the control plots only insectivores showed significant relationships with precipitation. The 2 guilds whose dynamics differed between the control and removal plots, granivores and folivores, also were the groups that increased in abundance on the treatments relative to controls during this period (Heske et al. 1994). However, we observed no difference between the rodent dynamics on control and removal plots in time period 1. This could be indicative of additional complexities or be a consequence of the lagged response of the rodent community to the treatment (Heske et al. 1994). Overall, these results lend further support to the contention of Lima et al. (2008) that the complex responses of rodents to precipitation at Portal is affected by the identity of sympatric species and that the kangaroo rats as a group have the greatest impact on these responses.

Complex interactions between changing vegetation and rodents.—No evidence of direct competitive effects of kangaroo rat removal on insectivores and folivores has been

found at the site (Heske et al. 1994). Thus, competition for space with kangaroo rats is an unlikely mechanism to account for the changing temporal relationship between precipitation and community dynamics in these guilds. This suggests that underlying, long-term changes in the ecosystem also could be influencing rodent populations. One of the striking long-term changes at Portal likely to influence various aspects of small mammal ecology is the >3-fold increase in shrub density (Brown et al. 1997) characteristic of desertification in arid systems throughout the world (Van Auken 2000).

Because resource availability to rodents is determined by plant response to precipitation, shifts in vegetation, such as increasing shrub cover, could impact the magnitude and timing of how precipitation is translated into resources. Previous studies have shown that communities dominated by different types of vegetation (i.e., grassland, shrubland, or woodland) will exhibit different lags in rodent responses to precipitation (Ernest et al. 2000). Unfortunately, we do not have data on actual resource availability (e.g., seed densities and insect abundances) and so rely on trends in plant abundances through time as a surrogate. Plant abundances consistently have shown positive relationships with precipitation at Portal (Fig. 3; Ernest et al. 2000), as seen in many arid systems (Ernest et al. 2000; Inouye 1991; Meserve et al. 2003; Schwinning and Sala 2004). However, these relationships are not particularly strong, indicating a surprising degree of complexity in the response of the primary producers at Portal, as also seen in Guo et al. (2002). As we expected to see with energy use of rodents relative to abundance, we expect that an alternative measure that better approximated productivity of plants (e.g., cover or biomass) would exhibit stronger relationships with water inputs in this system. For example, no dramatic increase in plant abundance was seen following the record precipitation in the summer of 2006; however, photographs indicate that the biomass of individual plants was exceedingly high (Fig. 4).

Coarse measurements of primary productivity probably only partially explain the variability in changes in plant abundance in response to precipitation. Previous work at the site demonstrated important interactions between summer and winter annual communities, despite only 1 or 2 species typically spanning both seasons. Guo and Brown (1997) found that a good season for one community of annual plants was commonly followed by a poor season for the other community, suggesting competition between these temporally disjunct plant communities. Because decomposition in desert ecosystems is slow, competition for soil nutrients locked in the slowly decaying biomass of the previous season was proposed as a possible explanation (Guo and Brown 1997; Gutierrez and Whitford 1987). However, it is possible the rodents themselves contribute to the complex dynamics of the plants. Granivorous and folivorous rodents that might increase in response to 1 good season could survive to impact the plant crop negatively the following season. The response to precipitation that lagged by 1 season, seen in the 2 herbivorous guilds, offers support to a key aspect of this hypothesis.

Regardless of the underlying mechanism, negative interactions between summer and winter annual plant communities further complicate responses to pulsed water resources at Portal.

In addition to these potential changes in bottom-up dynamics, increasing shrub densities could also alter top-down processes. Shrub cover is a key feature of the landscape to which many rodents respond, because rodents often concentrate their foraging activities under shrub canopies to decrease predation risk (Brown and Lieberman 1973; Kotler and Brown 1988). Although no data exist on predator abundances and predation rates at Portal, rodent population dynamics in other systems respond to changes in predation (Letnic et al. 2005; Lima et al. 2001; Meserve et al. 2003; Schmidt and Ostfeld 2008). If increased shrub cover does provide refuge from predators, however, it is possible that rates of predation have decreased over time, shifting control of rodent populations from predators to resources. This potential mechanism, if operating, likely would impact all guilds of rodents, because folivores, insectivores, and granivores all are vulnerable to the same suite of predators. The increasing influence of precipitation on dynamics of all guilds over time, coincident with increasing shrub density, is consistent with this mechanism.

Precipitation event size and timing.—Timing and distribution of precipitation also can contribute to complex dynamics of primary producers and consumers (Beatley 1974; Inouye 1991; Sala et al. 1992). For example, heavy rains early in the winter of 1999 produced many annual plant stems that season, but most annuals did not ultimately produce seeds, likely because of low precipitation throughout the remainder of the season (Brown and Ernest 2002). In other systems summer annuals are known to require little moisture to germinate, but survival and reproduction depend on precipitation after germination (Guo et al. 2002; Inouye 1991). In addition to timing, the magnitude of precipitation events affects how available water is partitioned among shrubs, grasses, and herbs in arid systems (Sala et al. 1992). Possible changes in precipitation regime, in terms of frequency and magnitude of precipitation events, coupled with increasing shrub densities at the site, could complicate the tested relationships.

One aspect of changing precipitation dynamics at Portal that is readily apparent in our analysis is the overall decreasing trend in seasonal precipitation since 1980. This is driven by increased variability in precipitation over time; no season before 1990 received less than 90 mm, but many seasons after 1990 did. This suggests an additional explanation for the changing relationship between plants and rodents. Arid systems subject to resource pulses might experience "threshold effects"—levels of resource availability above which biological responses are saturated (Schwinning and Sala 2004). In our system, above some critical amount of precipitation, rodent abundances might be more limited by some other critical resource. Our results are not inconsistent with this hypothesis. The lack of any significant relationships between precipitation and rodents during time period 1 could be related to the lack of extremely low seasonal precipitation.

Perhaps rodent abundance did not respond consistently to precipitation because responses of rodents were saturated at moderate levels of precipitation. However, as the system shifted and more seasons occurred with <90 mm of precipitation, this threshold might have been crossed, resulting in more marked declines and increased variability in rodent populations. Comparisons of rodent dynamics across gradients of precipitation variability (either temporal or spatial) could be very informative in determining whether desert rodent dynamics, like desert plant dynamics, are influenced by precipitation thresholds.

Conclusions: the continuing saga of rodents and precipitation.—Although the relationship between rodents and rain at our site has in some ways become stronger and clearer with almost 30 years of data, it also has been revealed to be more complex. Using the long-term observational data, we were able to detect differences among trophic guilds in their response to precipitation events, but it is clear that the nature of these relationships has been changing through time. We have discussed what we believe to be the most likely potential factors contributing to the complex, changing relationships between precipitation, plants, and rodent consumers for which we have at least some data. However, ecosystems are by their nature complicated, and other contributing factors are possible, including complex dynamics of predators (Meserve et al. 1996; Polis et al. 1998), parasites (Ostfeld 2008), and nonrodent competitors for seeds, vegetation, and insects (Brown and Davidson 1977; Brown et al. 1979; Pianka 1986). In addition, we have assumed relatively linear relationships between rodents and precipitation with our analyses. Nonlinearities in population dynamics can obscure the effect of climatic variation on population fluctuations; for example, precipitation and population density can act in concert to determine total population sizes (Berryman and Lima 2006; Lima et al. 2008). Lima et al. (2008) found evidence of such nonlinearities in an analysis of long-term population dynamics of *D. merriami* and *D. ordii* at Portal, with intraspecific density dependence and summer precipitation together accounting for 60–71% of the observed variation in population size. It remains an open question whether these types of nonlinear responses also can influence whole community dynamics.

Although incorporation of any or all of these additional mechanisms could clarify the dynamics of rodent populations by accounting for significant portions of the variation, it does not change the simple conclusion that no simple, linear relationship between precipitation and rodent response transcends the complexities of this ecosystem. Instead, our results suggest that the responses of consumers to precipitation in deserts could be changing in response to the numerous perturbations that desert ecosystems are experiencing. Portal has shown that the global phenomena of changing precipitation regimes, increasing frequency of extreme climatic events, and shrub encroachment can interact to reorganize communities and consequently ecosystem dynamics. Further exploration of the mechanisms underlying such reorganization is critical to understanding the long-term consequences of global climate change in arid systems.

LITERATURE CITED

ANDERSON, W. B., D. A. WAIT, AND P. STAPP. 2008. Resources from another place and time: responses to pulses in a spatially subsidized system. Ecology 89:660–670.

BEATLEY, J. C. 1969. Dependence of desert rodents on winter annuals and precipitation. Ecology 50:721–724.

BEATLEY, J. C. 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55:856–863.

BERRYMAN, A., AND M. LIMA. 2006. Deciphering the effects of climate on animal populations: diagnostic analysis provides new interpretation of Soay sheep dynamics. American Naturalist 168:784–795.

BRADY, M. J., AND N. A. SLADE. 2004. Long-term dynamics of a grassland rodent community. Journal of Mammalogy 85:552–561.

BROWN, J. H. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. Ecology 54:755–787.

BROWN, J. H. 1975. Geographical ecology of desert rodents. Pp. 315–341 in Ecology and evolution of communities (M. L. Cody and J. M. Diamond, eds.). Harvard University Press, Cambridge, Massachusetts.

BROWN, J. H. 1998. The desert granivory experiments at Portal. Pp. 71–95 in Issues and perspectives in experimental ecology (W. L. Resetarits, JR., and J. Bernardo, eds.). Oxford University Press, Oxford, United Kingdom.

BROWN, J. H., AND D. W. DAVIDSON. 1977. Competition between seed-eating rodents and ants in desert ecosystems. Science 196:880–882.

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

BROWN, J. H., AND B. A. HARNEY. 1993. Population and community ecology of heteromyid rodents in temperate habitats. Pp. 618–651 in Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication 10, The American Society of Mammalogists.

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

BROWN, J. H., AND G. A. LIEBERMAN. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. Ecology 54:788–797.

BROWN, J. H., O. J. REICHMAN, AND D. W. DAVIDSON. 1979. Granivory in desert ecosystems. Annual Review of Ecology and Systematics 10:201–227.

BROWN, J. H., T. J. VALONE, AND C. G. CURTIN. 1997. Reorganization of an arid ecosystem in response to recent climate change. Proceedings of the National Academy of Sciences 94:9729–9733.

CHASE, J. M., M. A. LEIBOLD, A. L. DOWNING, AND J. B. SHURIN. 2000. The effects of productivity, herbivory, and plant species turnover in grassland food webs. Ecology 81:2485–2497.

CHESSON, P., ET AL. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141:236–253.

CHEW, R. M., AND B. B. BUTTERWORTH. 1964. Ecology of rodents in Indian Cove (Mojave Desert), Joshua Tree National Monument, California. Journal of Mammalogy 45:203–225.

COLLINS, S. L., ET AL. 2008. Pulse dynamics and microbial processes in aridland ecosystems. Journal of Ecology 96:413–420.

DREVER, M. C., J. R. GOHEEN, AND K. MARTIN. 2009. Species–energy theory, pulsed resources, and regulation of avian richness during a mountain pine beetle outbreak. Ecology 90:1095–1105.

EASTERLING, D. R., G. A. MEEHL, C. PARMESAN, S. A. CHANGNON, T. R. KARL, AND L. O. MEARNS. 2000. Climate extremes: observations, modeling, and impacts. Science 289:2068–2074.

ENSCORE, R. E., ET AL. 2002. Modeling relationships between climate and the frequency of human plague cases in the southwestern United States, 1960–1997. American Journal of Tropical Medicine and Hygiene 66:186–196.

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

ERNEST, S. K. M., J. H. BROWN, K. M. THIBAULT, E. P. WHITE, AND J. R. GOHEEN. 2008. Zero sum, the niche, and metacommunities: long-term dynamics of community assembly. American Naturalist 172:E257–E269.

FITCH, H. S. 1948. Habits and economic relationships of the Tulare kangaroo rat. Journal of Mammalogy 29:5–35.

FOX, J. 2002. An R and S-plus companion to applied regression, Web appendix. Sage Publications, Thousand Oaks, California. http://socserv.mcmaster.ca/jfox/books/companion/appendix.html. Accessed 14 October 2008.

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.

GARCIA-MOYA, E., AND C. M. MCKELL. 1970. Contribution of shrubs to the nitrogen economy of a desert-wash plant community. Ecology 51:81–88.

GILLESPIE, S. C., D. H. VAN VUREN, D. A. KELT, J. M. EADIE, AND D. W. ANDERSON. 2008. Dynamics of rodent populations in semiarid habitats in Lassen County, California. Western North American Naturalist 68:76–82.

GOHEEN, J. R., E. P. WHITE, S. K. M. ERNEST, AND J. H. BROWN. 2005. Intra-guild compensation regulates species richness in desert rodents. Ecology 86:567–573.

GRINNELL, J. 1939. Effects of a wet year on mammalian populations. Journal of Mammalogy 20:62–64.

GUO, Q. F., AND J. H. BROWN. 1997. Interactions between winter and summer annuals in the Chihuahuan Desert. Oecologia 111:123–128.

GUO, Q. F., J. H. BROWN, AND T. J. VALONE. 2002. Long-term dynamics of winter and summer annual communities in the Chihuahuan Desert. Journal of Vegetation Science 13:575–584.

GUTIERREZ, J. R., AND W. G. WHITFORD. 1987. Chihuahuan Desert annuals—importance of water and nitrogen. Ecology 68:2032–2045.

HAFNER, M. S. 1977. Density and diversity in Mojave Desert rodent and shrub communities. Journal of Animal Ecology 46:925–938.

HESKE, E. J., J. H. BROWN, AND S. MISTRY. 1994. Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. Ecology 75:438–445.

HOFFMEISTER, D. F. 1986. Mammals of Arizona. University of Arizona Press and Arizona Game and Fish Department, Tucson.

INOUYE, R. 1991. Population biology of desert annual plants. Pp. 27–54 in The ecology of desert communities (G. Polis, ed.). University of Arizona Press, Tucson.

JAKSIC, F. M., S. I. SILVA, P. L. MESERVE, AND J. R. GUTIÉRREZ. 1997. A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America. Oikos 78:341–354.

KELT, D. A., J. A. WILSON, E. S. KONNO, J. D. BRASWELL, AND D. DEUTSCHMAN. 2008. Differential responses of two species of kangaroo rat (Dipodomys) to heavy rains: a humbling reappraisal. Journal of Mammalogy 89:252–254.

KOTLER, B. P. 1984. Risk of predation and the structure of desert rodent communities. Ecology 65:689–701.

KOTLER, B. P., AND J. S. BROWN. 1988. Environmental heterogeneity and the coexistence of desert rodents. Annual Review of Ecology and Systematics 19:281–307.

LETNIC, M., B. TAMAYO, AND C. R. DICKMAN. 2005. The responses of mammals to La Niña (El Niño Southern Oscillation)–associated rainfall, predation, and wildfire in central Australia. Journal of Mammalogy 86:689–703.

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.

LIMA, M., R. JULLIARD, N. C. STENSETH, AND F. M. JAKSIC. 2001. Demographic dynamics of a neotropical small rodent (Phyllotis darwini): feedback structure, predation and climatic factors. Journal of Animal Ecology 70:761–775.

LIMA, M., P. A. MARQUET, AND F. M. JAKSIC. 1999. El Niño events, precipitation patterns, and rodent outbreaks are statistically associated in semiarid Chile. Ecography 22:213–218.

LIMA, M., M. A. PREVITALI, AND P. L. MESERVE. 2006. Climate and small rodent dynamics in semi-arid Chile: the role of lateral and vertical perturbations and intra-specific processes. Climate Research 30:125–132.

LIMA, M., N. C. STENSETH, AND F. M. JAKSIC. 2002. Population dynamics of a South American rodent: seasonal structure interacting with climate, density dependence and predator effects. Proceedings of the Royal Society of London, B. Biological Sciences 269:2579–2586.

LIMA, M., N. C. STENSETH, H. LEIRS, AND F. M. JAKSIC. 2003. Population dynamics of small mammals in semi-arid regions: a comparative study of demographic variability in two rodent species. Proceedings of the Royal Society of London, B. Biological Sciences 270:1997–2007.

MANTOOTH, S. J., AND T. L. BEST. 2005. Chaetodipus penicillatus. Mammalian Species 767:1–7.

MESERVE, P. L., J. R. GUTIÉRREZ, J. A. YUNGER, L. C. CONTRERAS, AND F. M. JAKSIC. 1996. Role of biotic interactions in a small mammal assemblage in semiarid Chile. Ecology 77:133–148.

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.

MESERVE, P. L., ET AL. 1995. Heterogeneous responses of small mammals to an El Niño Southern Oscillation event in northcentral semiarid Chile and the importance of ecological scale. Journal of Mammalogy 76:580–595.

NAGY, K. A., I. A. GIRARD, AND T. K. BROWN. 1999. Energetics of free-ranging mammals, reptiles, and birds. Annual Review of Nutrition 19:247–277.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4:25–51.

Orland, M. C., and D. A. Kelt. 2007. Responses of a heteromyid rodent community to large- and small-scale resource pulses: diversity, abundance, and home-range dynamics. Journal of Mammalogy 88:1280–1287.

Ostfeld, R. S. 2008. Parasites as weapons of mouse destruction. Journal of Animal Ecology 77:201–204.

Ostfeld, R. S., and R. D. Holt. 2004. Are predators good for your health? Evaluating evidence for top-down regulation of zoonotic disease reservoirs. Frontiers in Ecology and the Environment 2:13–20.

Pianka, E. R. 1986. Ecology and natural history of desert lizards. Princeton University Press, Princeton, New Jersey.

Polis, G. A. 1991. The ecology of desert communities. University of Arizona Press, Tucson.

Polis, G. A., S. D. Hurd, C. T. Jackson, and F. Sanchez-Pinero. 1998. Multifactor population limitation: variable spatial and temporal control of spiders on Gulf of California islands. Ecology 79:490–502.

Previtali, M. A., M. Lima, P. L. Meserve, D. A. Kelt, and J. R. Gutiérrez. 2009. Population dynamics of two sympatric rodent species in a variable environment: rainfall, resource availability, and predation. Ecology 90:1996–2006.

Randall, J. A. 1984. Territorial defense and advertisement by footdrumming in bannertail kangaroo rats (*Dipodomys spectabilis*) at high and low population-densities. Behavioral Ecology and Sociobiology 16:11–20.

Reynolds, H. G. 1958. The ecology of the Merriam's kangaroo rat (*Dipodomys merriami mearns*) on grazing lands of southern Arizona. Ecological Monographs 28:111–127.

Rosenzweig, M. L. 1968. Net primary productivity of terrestrial environments: predictions from climatological data. American Naturalist 102:67–84.

Rosenzweig, M. L., and J. Winakur. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology 50:558–572.

Sala, O. E., W. K. Lauenroth, and W. J. Parton. 1992. Long-term soil–water dynamics in the shortgrass steppe. Ecology 73:1175–1181.

Schmidt, K. A., and R. S. Ostfeld. 2008. Numerical and behavioral effects within a pulse-driven system: consequences for shared prey. Ecology 89:635–646.

Schwinning, S., and O. E. Sala. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141:211–220.

Shenbrot, G. I., K. A. Rogovin, and E. J. Heske. 1994. Comparison of niche-packing and community organization in desert rodents in Asia and North America. Australian Journal of Zoology 42:479–499.

Stapp, P., and G. A. Polis. 2003. Influence of pulsed resources and marine subsidies on insular rodent populations. Oikos 102:111–123.

Stenseth, N. C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. Oikos 87:427–461.

Thibault, K. M., and J. H. Brown. 2008. Impact of an extreme climatic event on community assembly. Proceedings of the National Academy of Sciences 105:3410–3415.

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.

Valone, T. J., J. H. Brown, and C. L. Jacobi. 1995. Catastrophic decline of a desert rodent, *Dipodomys spectabilis*: insights from a long-term study. Journal of Mammalogy 76:428–436.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics 31:197–215.

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.

White, E. P., and M. A. Gilchrist. 2007. Effects of population-level aggregation, autocorrelation, and interspecific association on the species–time relationship in two desert communities. Evolutionary Ecology Research 9:1329–1347.

Whitford, W. G. 1976. Temporal fluctuations in density and diversity of desert rodent populations. Journal of Mammalogy 57:351–369.

Yang, L. H. 2008. Pulses of dead periodical cicadas increase herbivory of American bellflowers. Ecology 89:1497–1502.

Yang, L. H., J. L. Bastow, K. O. Spence, and A. N. Wright. 2008. What can we learn from resource pulses? Ecology 89:621–634.

Yates, T. L., et al. 2002. The ecology and evolutionary history of an emergent disease: hantavirus pulmonary syndrome. BioScience 52:989–998.

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