

Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources

S. K. Morgan Ernest, James H. Brown and Robert R. Parmenter

Ernest, S. K. M., Brown, J. H. and Parmenter, R. R. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. – *Oikos* 88: 470–482.

Resource/consumer dynamics are potentially mediated by both limiting resources and biotic interactions. We examined temporal correlations between precipitation, plant cover, and rodent density, with varying time lags using long-term data from two sites in the Chihuahuan desert of North America: the Sevilleta Long-term Ecological Research site (LTER), New Mexico, USA and a site near Portal, Arizona, USA. We also calculated the spatial correlations in precipitation, plant cover, and rodent dynamics among six sites, five at Sevilleta and one at Portal. At Sevilleta, all three variables were temporally correlated, with plant cover responding to precipitation during the same growing season and rodent populations lagging at least one season behind. At Portal, plant stem count was also correlated with precipitation during the same growing season, but there was no significant correlation between rodents and either precipitation or plant growth. Spatial correlations in plant cover and rodent populations between sites reflected the localized nature of summer rainfall, so that sites with highly correlated summer precipitation exhibited higher correlations in plant cover and rodent populations. In general, our results indicate that limiting resources influence consumer dynamics, but these dynamics also depend crucially on the biotic interactions in the system.

S. K. M. Ernest, J. H. Brown and R. R. Parmenter, Dept of Biology, Univ. of New Mexico, Albuquerque, NM 87131, USA (mernest@unm.edu).

While the structure and function of ecosystems with multiple trophic levels are known to vary in both time and space, the processes causing this variation are much less well understood. The causes can include intrinsic mechanisms, such as stochastic variation (e.g., demographic stochasticity), positive and negative feedbacks (e.g., Allee effects, negative density dependence), and complex non-linear dynamics (e.g., low-dimensional chaos) (Turchin et al. 1991, Ostfeld et al. 1993). Temporal and spatial dynamics can also be influenced by variation in the abiotic environment. Such variation may affect some components of ecosystems either directly through fluctuations in abiotic environmental conditions (McClelland and Hain 1979, Chapin and Shaver 1985, Parmesan 1996, Mehlman 1997), or indirectly by influencing other organisms that are either resources, competitors, or consumers (Connell 1961,

Paine 1966, Vanni et al. 1990, Grant and Grant 1996). There is observational and experimental evidence for all of these processes, but their relative influence has been debated. For example, experimental manipulations of resources and consumers, especially in aquatic ecosystems, have demonstrated the importance of abiotic and biotic processes, but their relative and interacting influences on temporal and spatial variation in unmanipulated aquatic and terrestrial ecosystems remain poorly understood (Hairston et al. 1960, Murdoch 1966, Paine 1966, Ehrlich and Birch 1967, Schindler 1977, McCauley and Kalff 1981, Hanson and Peters 1984, McNaughton et al. 1989, Power 1990, 1992, Vanni et al. 1990, Hunter and Price 1992, Leibold et al. 1997).

Over large scales of time and space, the magnitude of differences in the structure and dynamics of ecosystems is often striking. Studies of the natural variation in

Accepted 5 July 1999

Copyright © OIKOS 2000

ISSN 0030-1299

Printed in Ireland – all rights reserved

ecosystems over long periods of time and large expanses of space can offer insights into how they respond to environmental variation. For example, many studies have related fluctuations in climate to population dynamics of single species, variation in species composition, and changes in ecosystem variables, such as productivity and biomass (e.g., Davis 1986, Graham 1986, Tilman and Downing 1994, Chapin et al. 1995, Grant and Grant 1996). Most of these studies, however, have focused on a single trophic level rather than attempting to follow the direct and indirect influences of climate through the trophic structure (but see Grant and Grant 1996, Meserve et al. 1996, Brown et al. 1997, Jaksic et al. 1997, Polis et al. 1998). If abiotic factors such as climate have such large effects on single populations or trophic levels, they would be expected to influence other trophic levels and the structure and dynamics of entire ecosystems, either directly or through indirect biotic interactions.

Arid ecosystems provide excellent opportunities for examining the effects of resource limitation at multiple trophic levels. Water is the ultimate limiting resource in arid systems. In the American Southwest, regional correlations in precipitation are implicated in large-scale pest outbreaks, synchronized wildfires, and shrub invasions of southwestern grasslands (Swetnam and Betancourt 1998). At a smaller scale, changes in primary production and animal populations in both time and space have also been attributed to patterns of precipitation (Tevis 1958a, b, Beatley 1967, 1969, 1974, Brown 1987, Sala et al. 1988, Meserve et al. 1995, Jaksic et al. 1997, Polis et al. 1998, Lima et al., 1999). While water availability may have direct influences on some species at higher trophic levels, its primary effect is on plants. Rainfall is usually followed, with relatively short time lags, by germination of annuals and growth and reproduction of both annuals and perennials. Consequently, large-scale variations in plant cover and primary production in arid ecosystems over both time and space are correlated with actual evapotranspiration, which varies closely with precipitation (Hillel and Tadmor 1962, Rosenzweig 1968). Variation in primary production, in turn, determines the availability of resources (including foliage, flowers, and seeds) to primary consumers such as herbivorous insects and granivorous rodents (Beatley 1969, Brown et al. 1979, Pianka 1986). Granivorous rodents are hypothesized to be mainly resource-limited and not predator controlled, strengthening the possible importance of fluctuations in resource availability to rodent population dynamics in arid systems (Slobodkin et al. 1967, Oksanen 1992). Fluctuations in rodent populations have further ramifications up food chains by affecting resource availability to secondary consumers. However, many of the studies on the relationship between rodent populations and resource availability are very limited in temporal and/or spatial scope and do not address how these correlations vary across different habitats and over longer timescales.

Through a combination of long-term temporal and large-scale spatial comparisons in arid ecosystems, it should be possible to determine how much of the variability in primary production and consumer populations can be explained by variability in the availability of limiting water resources. This has not generally been done. The studies (see previous citations) demonstrating resource limitation, both of water on plants and of primary productivity on consumers, have not typically focused on the long-term dynamics. These studies typically consist of observations of short duration and limited spatial extent. While water resources may be limiting, their effects on consumer dynamics may be complicated because of non-linearities in trophic interactions and influences of other factors. While variation in precipitation in desert ecosystems might be expected to result in closely correlated responses at other trophic levels, this prediction requires empirical testing. The extent to which resources and consumers are coupled has important implications, both for conceptual issues of ecosystem dynamics and for practical applications, such as understanding outbreaks of Hantavirus and Lyme disease (Parmenter et al. 1993, Ostfeld 1997).

Data from the Sevilleta LTER in central New Mexico and Brown's long-term study site in southeastern Arizona provide the opportunity to analyze resource/consumer dynamics over large scales of both time and space. Here we perform such an analysis at three levels: precipitation inputs, plant growth responses, and rodent population dynamics. Considering the trophic structure and possible temporal and spatial correlations among these components (Fig. 1), it is possible to make several a priori predictions:

- 1) To the extent that water is a limiting resource which affects producers and consumers through linear trophic responses, there should be positive correlations, with increasing time lags, linking precipitation, plants, and rodents. Following the notation in Fig. 1, we predict: a) r_{1A} and r_{1B} to be significant and positive; and b) r_{2A} , r_{3A} , r_{2B} , and r_{3B} also to be significant and positive, but after greater time lags.
- 2) To the extent that there is similarity between sites in amount and timing of precipitation, sites should also exhibit spatially correlated dynamics of plant and rodent response. That is, we predict $r_{P,A/B}$, $r_{C,A/B}$, and $r_{R,A/B}$ to be significant and positive.
- 3) Differences in spatial dynamics may be due to the patterns of winter and summer precipitation. Winter precipitation comes from broad frontal weather systems which move from west to east across the southwest (Mock 1996). Consequently, we expect significant correlations in winter precipitation among all sites on Sevilleta and perhaps between Sevilleta and Portal. In contrast, summer precipitation comes from convective thunderstorms which are often very localized (Mock 1996). Consequently, we predict significant correlations in summer precipitation only between sites in close

proximity. Furthermore, we expect that the spatial pattern of plant and rodent dynamics will reflect the extent to which they are influenced by the localized nature of summer precipitation.

4) If dynamics of producer and consumer populations are driven predominately by processes such as dispersal, instead of extrinsic forces such as climate, then the population dynamics of individual species and the pattern of species composition should be closely correlated among sites in close proximity. In such cases, fluctuations in producers and consumers might be more closely related to distance between sites than to similarity in climate.

5) If complex, non-linear influences within the trophic structure are present (e.g., strong cascading "top-down" effects of predators or strong density-dependent population control) they will tend to complicate, and perhaps to obscure, the response to variation in limiting resources due to fluctuations in precipitation.

Methods

Study areas

Data were obtained from both the Sevilleta LTER, 90 km south of Albuquerque, New Mexico and Brown's long-term research site in southeastern Arizona, located approximately 400 km southwest of the Sevilleta, and 7 km east of Portal, Arizona. Both areas are located at the transition between arid grassland and desert shrubland in the Chihuahuan Desert, and they have many of the same plant and animal species.

The Sevilleta LTER area is bisected into east and west halves by the Rio Grande. This study used three sites on the west side of the river and two sites on the east (Fig. 2). The east side sites included a Great Plains grassland (East Grass) and a Chihuahuan desert shrub-

land (East Shrub). On the west side of the river, the three sites were a Chihuahuan desert shrubland (West Shrub), a mixed grassland-shrubland (West Grass), and a juniper woodland in the foothills of the Sierra Ladrones (West Wood). The distances between sites ranged from 29 km (from West Wood to East Grass) to a few hundred meters (from West Grass to West Shrub and from East Grass to East Shrub). Data on climate, vegetation, and rodent populations at these Sevilleta LTER sites have been collected since 1989.

In contrast, the Portal area is only 20 ha and consists of 24 permanent plots of 0.25 ha each. The area is characterized by upper elevation Chihuahuan Desert shrubland vegetation. Rodents have been censused monthly since 1977. Counts of all species of annual plants have been conducted twice yearly since 1989 and meteorological data have been collected since 1980.

Meteorological data

Seven automated meteorological stations are situated around the Sevilleta. Monthly precipitation totals from the nearest station (0.1–3 km) to each rodent trapping site were used. One meteorological station at the Portal area has been in operation since 1980. In the Chihuahuan Desert region, there are two distinct rainy seasons (winter and summer). Winter precipitation was summed from October to March and summer precipitation from April to September.

Plant cover

On the Sevilleta, plant cover data from permanently marked line-transects in the vicinity of the rodent trapping sites were used. Vegetation was measured twice per year (spring and late summer), and followed the same schedule as the rodent sampling. Plant transect

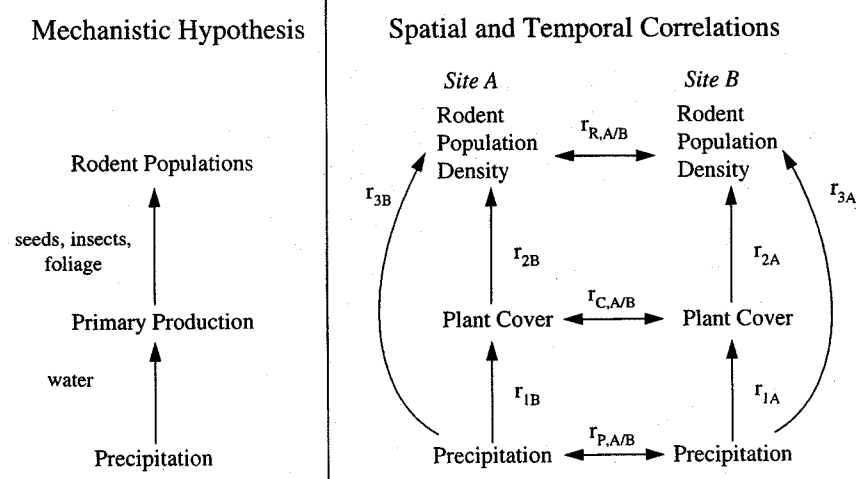
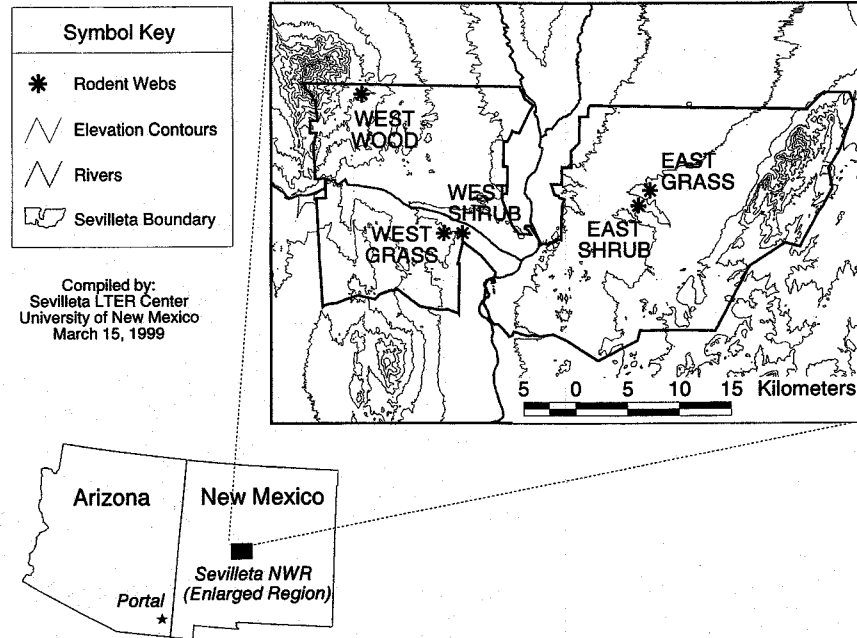


Fig. 1. Proposed mechanistic relationship between trophic levels and corresponding predictions of spatial and temporal correlations within and between two hypothetical sites, A and B, where r represents the correlation coefficient of specific comparisons.

Fig. 2. Map of Sevilleta Long-Term Ecological Research (LTER) area indicating sites used in this study.



lengths ranged from 400 m to 1000 m. Along each transect, total plant cover was measured by recording interceptions at 1-cm intervals. Total plant cover was calculated for each site and standardized by the length of the transect to yield a percent cover.

Three transect sites were used. One was immediately adjacent to the West Grass and West Shrub sites (West Plants), the second was near the East Grass and East Shrub sites (East Plants), and the third was nearest the West Wood site. To examine spatial correlations in vegetation cover, plant transects for a second site (Deep Well) on the east side of the Rio Grande were added.

At Portal, a plant census was conducted twice per year, after the growing season of winter annuals (March/April) and summer annuals (August/September). Plant stem counts for 16 quadrats, each 0.5 m² in area, for each plot were summed to yield a total stem count for the plot. An average density of stems for the site was obtained by calculating the average of the density of the 10 "control" plots (i.e., plots where rodent populations were not manipulated experimentally). The stem counts made at Portal and the line-transects measured at Sevilleta do not provide exactly comparable estimates of plant abundance. However, we do have both stem count and line transect data for some summers at Portal, and the two measures are highly correlated ($r = 0.86$, $P = 0.007$; unpubl.).

Rodent populations

At each of the five sites on the Sevilleta LTER, three permanent mark-recapture trapping webs were spaced

at least 100 m apart. Each web consisted of 12 rows of 12 stakes radiating out from a central point to cover 3.14 ha (see Parmenter et al. 1998 for details). Webs were trapped with Sherman live traps twice each year for three nights. From 1989 to 1993, trapping occurred once in May or June and again in July or August; beginning in 1994, the second trapping period was in September or October. Data from 1989 to 1996 were used for this study. Normally, rodent density estimates would be derived using various mathematical models (Buckland et al. 1993); however, to compute densities comparable to those from Portal data, the rodent density per web was calculated by dividing total number of unique individuals captured by the area covered by the web. Individuals captured more than once over the three nights were counted only once and few new individuals are caught on the third night. Total density of all species at each site for each trapping period was calculated by taking the average density for the three webs.

At Portal, we only used data from the 10 control plots which have been accessible to all rodent species since 1977. Each plot has a rectangular grid of seven permanent stakes in seven rows, with each stake separated by 6.25 m. Plots have been sampled once per month for 20 years (for details see Brown 1998 and included references). An average density of all rodent species for the site was calculated by taking the average of all plots and dividing by the total area (2.5 ha). Portal data were summarized in two ways. For comparisons with the Sevilleta, Portal data were categorized to match the timing of the Sevilleta trapping regime. Density was averaged for May/June for the first season

and either July/August or September/October for the second season. For internal comparisons of rodents at Portal with local precipitation and plant data, the two seasons consisted of three-month averages with April/May/June comprising the first season and September/October/November the second.

In this study, we were interested in the dynamics of resources and consumers through time and across space, not in how many consumers were supported by various amounts of resource. Therefore, we were less concerned about the exact densities of rodents than the fluctuations in community abundance. Since biases in density estimates attributable to trapping method and to influence of area outside the trapping grids are presumably consistent through time, they should not affect the correlations in fluctuations between sites or through time at one site.

At both study areas, the rodent fauna is dominated by granivores and omnivores. Species present at both the Sevilleta and Portal areas include: *Dipodomys merriami*, *D. ordii*, *D. spectabilis*, *Perognathus flavus*, *Peromyscus maniculatus*, *P. eremicus*, *Onychomys leucogaster*, and *Neotoma albigula*.

Statistical analyses

For every year, there were data for precipitation, plant cover, and rodent density for two seasons for each site. The two seasons were roughly equivalent for each variable. At both areas, the precipitation season did not always correspond exactly to the timing of the plant and rodent sampling. Therefore the season of precipitation overlapping and/or immediately preceding a sampling period for plants and rodents was considered to be the "same" season.

All correlation analyses in this paper were done using the Spearman rank correlation procedure in SAS. Although many correlations were calculated, we did not perform a Bonferroni correction. We were concerned with the overall pattern of variation, not whether any particular correlation coefficient exceeded some arbitrary $P < 0.05$ level of "statistical significance". Furthermore, for the hypotheses tested and the data used in this study, a Bonferroni adjustment is not appropriate. For testing for concordant patterns among systems in addressing a hypothesis, techniques such as meta-analysis or consensus testing are more appropriate (e.g., Rice 1990, Arnqvist and Wooster 1995). Such analyses test whether multiple data sets support or refute a hypothesis, which is what we are attempting to do. However, these techniques assume that the data sets are independent of one another. While the sites used are located in different habitats and have different community composition, they are not independent. There is substantial overlap in the species present and spatial covariation in environmental conditions. This precludes

the use of these types of analyses. Path analysis was also not appropriate due to the small sample sizes and the lack of experimental manipulations (Smith et al. 1997, 1998, Grace and Pugsek 1998).

Temporal correlations

Correlations were calculated to compare the relationships between plant cover and precipitation, rodent density and plant cover, and rodent density and precipitation for each of the sites. For each relationship, four different exploratory correlations were run: same season for response and predictor variables ($n = 15$ for each site), predictor variable from the season before the response variable ($n = 14$ for each site), predictor variable being the sum of the previous and same season as the response variable ($n = 14$ for each site), and predictor being the sum of the two seasons before the response variable ($n = 13$ for each site). In terms of the series analysis, these were nonparametric (Spearman) cross-correlations with varying time lags. For temporal correlations at Portal, rodent data since 1989 were used for comparisons with vegetation and precipitation.

Spatial correlations

Data on average rodent densities for each sample period at each of the sites were analyzed to determine the degree of temporal correlation across space. The data from 1989 to 1996 for each of the six rodent study areas were used. Spatial correlations were also conducted on the plant data across all sites and on the precipitation data using summer and winter precipitation totals. These spatial comparisons of time series data were nonparametric (Spearman) cross-correlations with zero time lags.

Community comparisons

Rodent species composition, consisting of the abundance (total captures of unique individuals) of each species, for all webs at each site for each season at the Sevilleta from 1989 to 1996 ($n = 48$, for each site) was used to compare the similarity of communities across the study area. The average relative abundance of each species at each site for the 1989–1996 time period was calculated and used to rank species in order of dominance. Spearman rank correlations were calculated to compare the ranks of the species in the communities among the sites. Correlation coefficients were plotted against the distance between the sites to assess effects of spatial proximity on community similarity.

Results

Temporal correlations

At all Sevilleta sites, there were consistent correlations among rodent density, plant cover, and precipitation

(Fig. 3). At the grass and shrub sites, percent plant cover was significantly correlated only with the precipitation from the same season. Plant cover at the Wood site was only significantly correlated with the total precipitation from the same and previous season. Rodent populations were correlated with plant cover and precipitation, but only after a time lag. At three sites, the highest correlations were between rodent density and the sum of precipitation in the previous two seasons. At each site, the correlations between plant cover and rodent density closely followed the relationship between rodent density and precipitation (Table 1). So, for example, if rodents at a site were most highly correlated with rainfall of the previous season, they were also most highly correlated with plant cover of the previous season.

At Portal, plant stem count was highly correlated with precipitation of the same season ($r = 0.78$, $P < 0.001$), but rodent density was not significantly correlated with either precipitation or vegetation (Fig. 3).

Spatial correlations

Comparisons of rodent densities across the Sevilleta revealed high correlations among the three sites on the west side and between the two sites on the east side, but weaker correlations between the two sides of the Rio Grande (Fig. 4). Portal exhibited highly negative correlations with sites on the west side of the Sevilleta, but no correlations with sites on the east. Vegetation cover was correlated on the same side of the river at the Sevilleta, but not between the two sides (Fig. 5). Plant stem count at Portal was not correlated with vegetation cover at any sites on the Sevilleta. Winter precipitation was highly correlated across the Sevilleta (Fig. 6). Summer precipitation was not correlated between the sites on the east and west sides of the river (Fig. 6). In

winter, but not summer, precipitation at Portal was weakly correlated with precipitation on the east and west sides of the Sevilleta.

Community comparisons

Sites of different habitat (grass or shrub) only a kilometer apart at Sevilleta had conspicuously different rodent communities (Table 2). Correlation coefficients comparing the rankings of species from 1989 to 1996 at different sites showed that there was an effect of distance on community similarity (Fig. 7). Nearby sites had similar composition, but at distances greater than 10 km there was also a high degree of variability in community composition not accounted for by distance.

Discussion

In general, the results support those predictions based on the premise that resource and consumer dynamics are governed primarily by variation in a limiting resource. With respect to temporal patterns, at all sites on Sevilleta there were correlations between precipitation and both plant cover and rodent populations. Correlations between plant cover and rodent populations were significant for three of the five sites, and almost significant for the other two, especially considering the small number of years. At Portal, there was a significant correlation only between precipitation and plant density; rodent populations were not correlated with either precipitation or plant density.

Increasing time lags in the correlations up the trophic chain also suggest that the dynamics were strongly influenced by inputs of limiting water resources. At Portal and four of the five sites at Sevilleta, plant responses were most closely correlated with precipita-

Fig. 3. Temporal cross-correlations between precipitation and plant cover, precipitation and rodent populations, and rodent populations and plant cover for Portal and each of five sites at the Sevilleta LTER. Dashed arrows are non-significant correlations. Solid arrows denote correlations with $P < 0.05$, bold arrows denote correlations with $P < 0.01$. The time lags of the correlations differed and are given in Table 1.

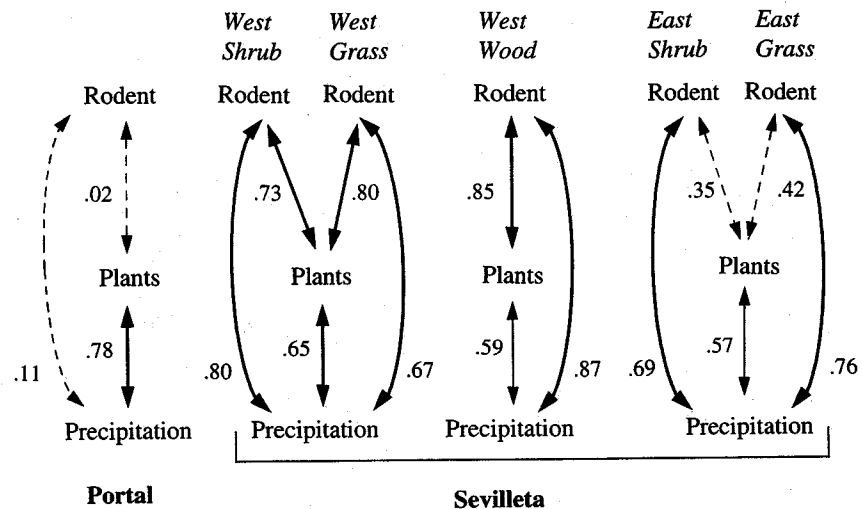


Table 1. Lag between response and predictor variables that yielded the highest correlation between plant cover and precipitation, rodents and plant cover, and rodents and precipitation. Lags in italics were marginally non-significant ($0.05 < P < 0.15$).

Sites	Plant cover and precipitation	Rodents and plant cover	Rodents and precipitation
East Grass	Same season	<i>Two previous seasons</i>	Two previous seasons
East Shrub	Same season	<i>Two previous seasons</i>	Two previous seasons
West Grass	Same season	Previous season	Previous season
West Shrub	Same season	Same plus previous season	Same plus previous season
West Wood	Same plus previous season	Two previous seasons or Same plus previous season	Two previous seasons
Portal	Same season	ns	ns

tion during the same growing season. At the highest elevation site on Sevilleta, West Wood, where temperatures are lower and soil moisture is probably higher and less temporally variable, plant cover was slightly better correlated with total precipitation during the same and previous growing seasons. At all Sevilleta sites rodent populations were correlated with, but lagged behind, plant growth. Lags in rodent response to plant growth varied as reflected in the seasonal plant cover that yielded the highest correlation: ranging from the same and previous seasons to the two previous seasons. This suggests that timing of rodent response to precipitation events may be mediated by the species composition of the vegetation, despite the fact that percent cover at almost all sites responded in the same season that the precipitation occurred. At all sites, lags between precipitation input and rodent response that gave the highest correlations were identical to lags that gave the highest correlations between rodent populations and plant cover.

Spatial patterns of correlations of timing and amount of precipitation, plant growth, and rodent response also suggest that limiting resources are important in the dynamics of these systems. At the Sevilleta, winter precipitation was highly correlated among all sites, but summer precipitation was significantly correlated only between sites on the same side of the river valley. Vegetation cover and rodent populations showed the same pattern, with correlations being substantially higher between sites on the same side of the river valley. Two features of these spatial patterns are especially noteworthy. The first is that summer precipitation was correlated only among sites on the same side of the Rio Grande. This can be attributed to the influence of topography, especially the mountain ranges that run parallel to the river, on the formation of convective storms and the resulting distribution of precipitation. The second pattern was that this spatial variation in summer precipitation appeared to greatly influence plant and rodent dynamics. Like precipitation, plant cover and rodent populations were most strongly correlated between sites on the same side of the river valley. This is further evidence for the dependence of produc-

ers and consumers on the temporal and spatial distribution of limiting water resources.

Winter precipitation at Portal was correlated with that at the sites on the Sevilleta, but there were no such correlations for summer precipitation. Neither rodent nor vegetation response at Portal were correlated with these variables at Sevilleta. Given the distance between Portal and Sevilleta (400 km), the relative independence of their resource and consumer dynamics is not surprising. More perplexing, however, is the fact (noted above) that at Portal rodent population dynamics were not correlated with either plants or precipitation. The high correlation between plant stem density and precipitation is evidence that production is limited by water availability at Portal as well as at Sevilleta. But it is clear that variation in precipitation did not lead to a correlated rodent response at Portal, even though it did so at Sevilleta. At Portal, Brown and Heske (1990a) noted an apparent coincidence of three peaks in rodent populations and three El Niño events of high winter precipitation in the 1980s. Two additional El Niño events in the early 1990s, however, were coincident with low and declining rodent populations (Brown 1998).

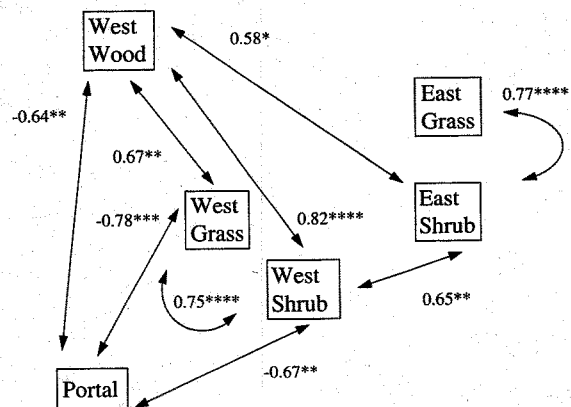


Fig. 4. Cross-correlations of rodent dynamics from 1989 to 1996 among five sites at the Sevilleta LTER and Portal. Only significant r -values from Spearman rank correlations are shown: *, $P < 0.05$, **, $P < 0.01$, ***, $P < 0.001$, ****, $P < 0.0005$.

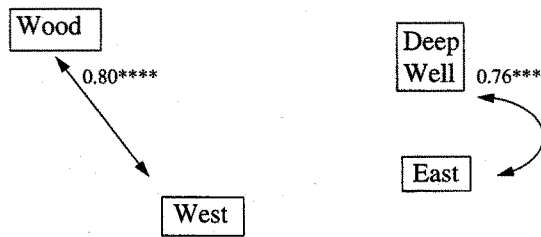


Fig. 5. Cross-correlations of vegetation cover from 1990 to 1996 among four sites at the Sevilleta LTER and Portal. Only significant r -values from Spearman rank correlations are shown: ***: $P < 0.001$, ****: $P < 0.0005$.

Neither of these reports included quantitative analyses of responses of rodents to either precipitation or plants. The present study indicates that these responses are not as closely coupled at Portal.

The seeming failure of rodent populations at Portal to track local fluctuations in resource availability suggests that their dynamics are complex, and probably more complex than at Sevilleta. We can envision several possibilities. One is top-down regulation, presumably due to rodent predators, which may have their own complex dynamical relationships with prey populations, primary production, and limiting resource supply (Paine 1966, Estes and Palmisano 1974, Lubchenco 1978, Meserve et al. 1996, Polis et al. 1998). Although we have no data on predator populations at Portal, it is possible that differences in predator abundance, perhaps due in part to previous rodent populations, could substantially affect rodent responses to fluctuations in resource availability. Though we have no data to assess this hypothesis, results from an arid ecosystem in South America suggest that strong predator control on rodent

response to fluctuations in resource is possible (Meserve et al. 1996; but see Jaksic et al. 1997). Another possibility is competitive interactions with other taxa of consumers, such as granivorous ants and birds, folivorous rabbits, ungulates, and insects, and insectivorous birds and reptiles (Brown and Davidson 1977, Brown et al. 1979, Pianka 1986). Complex dynamical influences of such competitors might be expected if the magnitude and timing of their responses to fluctuations in resource availability differ from those of rodents. A third possibility is that the fluctuations in rodent populations reflect non-linearities in intrinsic processes. An example would be chaotic dynamics due to intrinsic time lags or feedbacks in population dynamics and the interactions mentioned above (Hastings et al. 1993). Whatever the cause, however, we have no ready explanation why consumer/resource dynamics were seemingly uncoupled at Portal, in apparent contrast to the situation at Sevilleta. Even at the Sevilleta the correlations between resource and consumer dynamics, while "statistically significant", accounted for only a modest proportion of the variation: 12 to 72% for precipitation and plants, 32 to 42% for plants and rodents, and 45 to 76% for precipitation and rodents (Fig. 3). Inspection of the dynamical patterns also suggests that complex non-linear processes probably occurred at the Sevilleta as well as at Portal (Fig. 8).

Intrinsic dynamics, such as dispersal, could potentially explain correlations in rodent dynamics between sites in close proximity (Sutcliffe et al. 1996). When populations of the same species occurred at adjacent sites at Sevilleta their dynamics were indeed closely correlated (unpubl.). In general, however, the adjacent sites, which were in different habitats, had substantial differences in species composition. Nevertheless, the

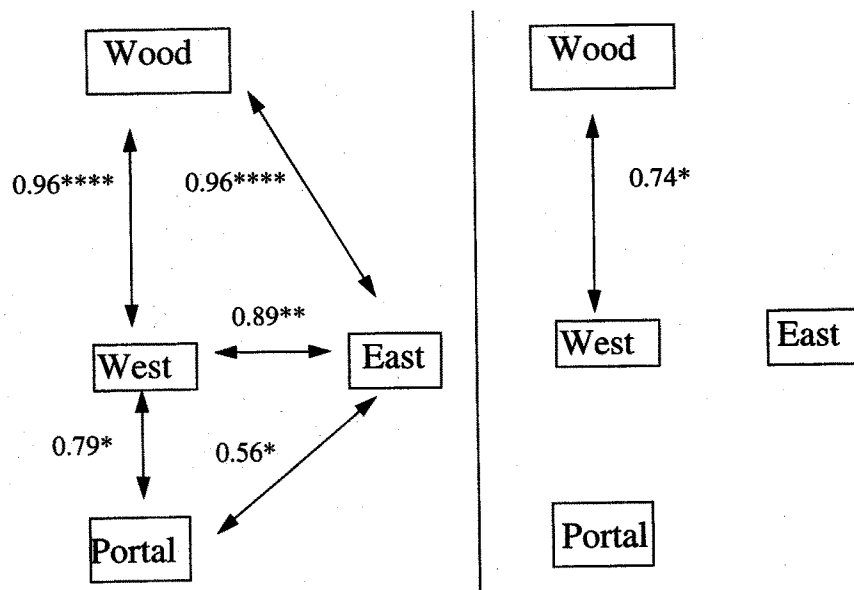


Fig. 6. Cross-correlations for winter (left) and summer (right) precipitation among three sites at the Sevilleta LTER and Portal. Only significant r -values from Spearman rank correlations are shown: *: $P < 0.05$, **: $P < 0.01$, ****: $P < 0.0005$.

Table 2. Ranks and mean relative abundance for the most abundant rodent species at sites on the Sevilleta (1989–1996). A + indicates that the species was present at the site.

Species	East Grass	East Shrub	West Shrub	West Grass	West Wood
<i>Chaetodipus intermedius</i>		+		+	2 (0.21)
<i>Dipodomys merriami</i>	+	1 (0.63)	1 (0.53)	2 (0.16)	1 (0.42)
<i>D. ordii</i>	2 (0.28)	+	7 (0.03)	1 (0.34)	+
<i>D. spectabilis</i>	3 (0.24)	2 (0.11)	+	+	+
<i>Neotoma albigula</i>	+	7 (0.02)	5 (0.04)	3 (0.16)	3 (0.14)
<i>N. mexicana</i>				+	+
<i>N. micropus</i>	6 (0.02)	+	+		+
<i>Onychomys arenicola</i>	4 (0.04)	4 (0.04)	+	6 (0.05)	+
<i>O. leucogaster</i>	+	+	+	5 (0.07)	+
<i>Perognathus flavescens</i>	+	+	+	4 (0.10)	7 (0.02)
<i>P. flavus</i>	1 (0.32)	3 (0.09)	2 (0.14)	+	5 (0.06)
<i>Peromyscus boylii</i>		+	+	+	+
<i>P. difficilis</i>	+	+	+	+	+
<i>P. eremicus</i>	+	5 (0.04)	+	+	+
<i>P. leucopus</i>	+	+	3 (0.07)	7 (0.04)	6 (0.03)
<i>P. maniculatus</i>		+	+	+	+
<i>P. truei</i>	7 (0.02)	6 (0.02)	4 (0.05)	+	4 (0.07)
<i>Reithrodontomys megalotis</i>	+	+	6 (0.03)	+	
<i>R. montanus</i>	5 (0.04)	+	+		

total abundances of all rodent species exhibited substantial spatial autocorrelation, and much of this was due to positive correlations between the different species that were dominant at adjacent sites. For example, on the east side, *D. merriami* was the dominant species at East Shrub, whereas *P. flavus* was most abundant at East Grass, and their populations were significantly correlated ($r = 0.78$, $P = 0.0003$). Similarly, on the west side, populations of the two dominant species, *D. merriami* at West Shrub and *D. ordii* at West Grass, were also positively correlated ($r = 0.49$, $P = 0.057$). This supports results reported earlier from Portal, where the vast majority of coexisting rodent species exhibited positively correlated population dynamics (Brown and Heske 1990a, Valone and Brown 1996). The patterns of spatial and temporal dynamics observed in this study suggest that most rodent species responded directly to fluctuations in food supply, but the dynamics of the different species were positively correlated, because food availability depended on previous episodes of primary production and precipitation. Thus, fluctuations in total abundance of all rodent species appeared to provide an integrated measure of food availability for this important group of consumers at Sevilleta, but perhaps less so at Portal for the reasons mentioned above.

Temporal and spatial patterns of precipitation input, plant growth, and rodent populations provide evidence for the influence of resource supply on consumer dynamics. However, the strength of that influence, especially on higher trophic levels, varied between study areas. At Sevilleta, there was evidence of a direct linear effect of resource limitation from climatic input through primary producers to rodent consumers. At Portal, there was a similar relationship between climate and primary producers, but no evidence of a direct

linear effect that carried through to the consumers. The non-linear relationship between rodents and their resources may reflect the influence of complex intra- and inter-specific interactions. This is especially interesting given that current theory on the regulation of trophic levels suggests that granivores should be regulated only by resource availability (Slobodkin et al. 1967, Oksanen 1992). Our results indicate that perhaps more attention should be paid to the importance of predators and competition in regulating the granivore trophic level. In general, however, our results are consistent with earlier, shorter term studies in arid ecosystems that linked plant

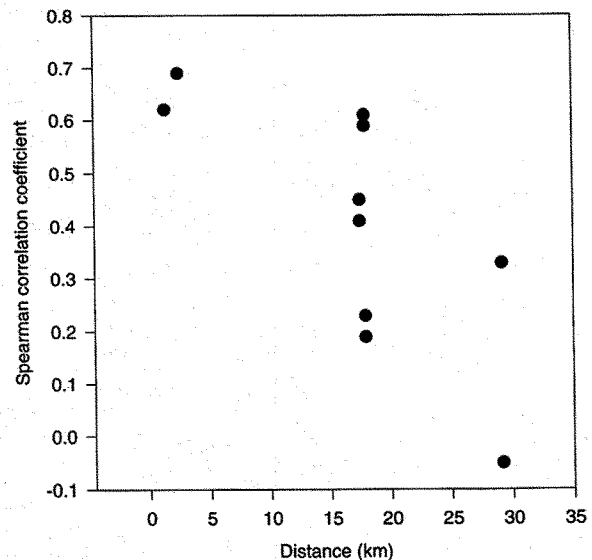
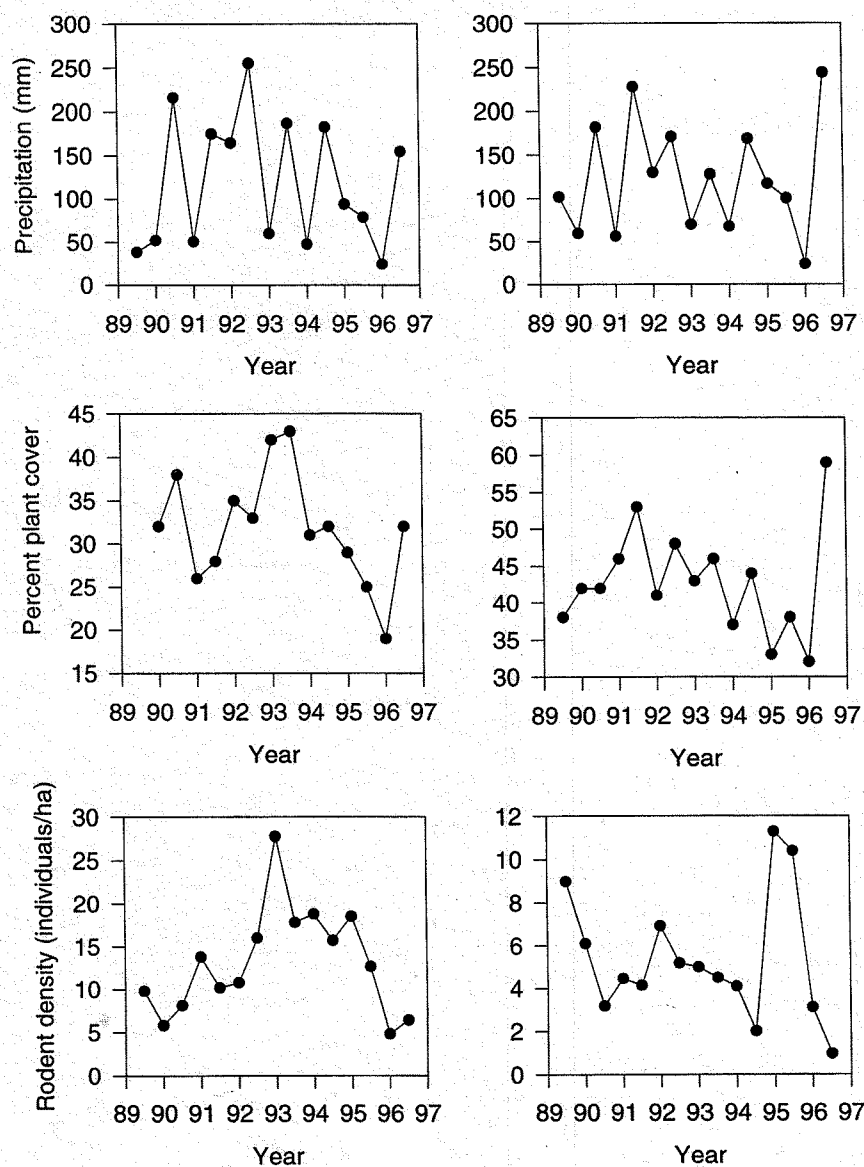


Fig. 7. Spearman rank correlation coefficient showing how rodent species composition, measured by ranked abundance, varied among sites as a function of the distance (km) between them.

Fig. 8. Precipitation, percent plant cover, and rodent density at two of the sites on the Seville: West Grass (left) and East Grass (right). While the time series for all three variables were significantly correlated at each site (except for rodents and plants at East Grass, see Fig. 3), inspection of the data indicates that resource/consumer relationships can account for only a modest proportion of the dynamics.



growth and rodent population dynamics to temporally varying precipitation (e.g., Chew and Butterworth 1964, Beatley 1969, Brown 1973, 1987, Whitford 1976, Hafner 1977, Meserve et al. 1995, Jaksic et al. 1997). Our results also point, however, to the unique insights afforded by long-term studies and large-scale spatial comparisons – that the resource/consumer dynamics are mediated by differences in habitat and that the strength of the relation between input of limiting resource and response by the rodent consumers may not be as strong as shorter-term studies might suggest. We should gain increased understanding of the processes that govern resource/consumer dynamics in these arid ecosystems as we acquire a longer record at both Seville and Portal.

A general message is that the dynamics of multiple interacting species or trophic levels may be more complicated than suggested by short-term experimental and non-manipulative studies. Even though the interactions documented in these studies may be strong, their effects on the structure and dynamics of multi-species systems may result in complex patterns of spatial and temporal variation. Because the different species interact with different components of the abiotic and biotic environment on different spatial and temporal scales, the dynamics of these systems are inherently non-linear and difficult to predict (Hastings et al. 1993, Brown et al. 1997). A case in point is the outbreak of diseases (Schaffer and Kot 1985, Olsen and Schaffer 1990). Recent studies have linked outbreaks of Hantavirus

and Lyme disease to linkages between climate, food resources, mammalian host populations, and pathogen transmission (Parmenter et al. 1993, Ostfeld 1997). While these linkages have probably been correctly identified, predictions about long-term dynamics, necessarily based on relatively short-term studies, should be treated with caution.

Results of this study complement and extend our understanding of trophic structure and dynamics. There has been much discussion of the roles of resource limitation and other processes, such as predation, in regulating the species composition of trophic levels and the flows of energy and materials through ecosystems (Hairston et al. 1960, Murdoch 1966, Paine 1966, Ehrlich and Birch 1967, Oksanen et al. 1981, Vanni 1987, Carpenter and Kitchell 1988, Leibold and Wilbur 1992, Power et al. 1996). Tests of these ideas tend to be of limited duration and restricted to single sites, and as a consequence have focused largely on trophic structure and short-term dynamics. The present study, based on data from multiple years and spatially disperse sites, provides a different perspective. On the one hand, long-term studies of single sites show how fluctuations in resource supply due to variation in the abiotic environment are transmitted from lower to higher trophic levels. On the other hand, comparison across multiple sites reveals system-specific variations in these dynamics, notably differences in time lags among sites at Sevilleta and differences in rodent response between Sevilleta and Portal. Furthermore, while this study provides strong evidence for resource limitation, other data provide equally strong evidence for other processes. In particular, the experimental manipulations of rodents at Portal demonstrate that these consumers strongly influence species composition, seed size, and other characteristics of the primary producers (Brown et al. 1986, Brown and Heske 1990b, Samson et al. 1992, Heske et al. 1993, Guo and Brown 1996). Taken together, our studies of trophic interactions in arid ecosystems support the conclusions of Hunter and Price (1992), Leibold et al. (1997), and others. Resource limitation interacts with predation and other processes to influence trophic structure and dynamics.

Acknowledgements – We thank the U.S. Fish and Wildlife Service and the Sevilleta LTER for use of their long-term data and facilities. We also thank Lauri Oksanen and Fabian Jaksic for reviewing the manuscript and giving us helpful feedback, Mathew Leibold for comments on the manuscript, E. Siemann for assistance, advice, and comments, D. M. Kaufman, F. A. Smith, J. J. Hamilton, and B. Enquist for discussion, G. MacKiegan for assistance in obtaining data, and G. Shore for creating the map of Sevilleta. This work was supported in part by NSF Grants DEB-9707406, BSR 88-11906, and DEB-9411976.

References

- Arnqvist, G. and Wooster, D. 1995. Meta-analysis: synthesizing research findings in ecology and evolution. – *Trends Ecol. Evol.* 10: 236–240.
- Beatley, J. C. 1967. Survival of winter annuals in the northern Mojave desert. – *Ecology* 48: 745–750.
- 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.
- Brown, J. H. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. – *Ecology* 54: 755–787.
- Brown, J. H. 1987. Variation in desert rodent guilds: patterns, processes, and scales. – In: Gee, J. H. R. and Giller, P. S. (eds), *Organization of communities past and present*. Blackwell, Oxford, pp. 185–204.
- Brown, J. H. 1998. The desert granivory experiments at Portal. – In: Resetarits, W. L., Jr. and Bernardo, J. (eds), *Issues and perspectives in experimental ecology*. Oxford Univ. Press, Oxford, pp. 71–95.
- Brown, J. H. and Davidson, D. W. 1977. Competition between seed-eating rodents and ants in desert ecosystems. – *Science* 196: 880–882.
- Brown, J. H. and Heske, E. J. 1990a. Temporal changes in a Chihuahuan desert rodent community. – *Oikos* 59: 290–302.
- Brown, J. H. and Heske, E. J. 1990b. Control of a desert-grassland transition by a keystone rodent guild. – *Science* 250: 1705–1707.
- Brown, J. H., Reichman, O. J. and Davidson, D. W. 1979. Granivory in desert ecosystems. – *Annu. Rev. Ecol. Syst.* 10: 201–228.
- Brown, J. H., Davidson, D. W., Munger, J. C. and Inouye, R. S. 1986. Experimental community ecology: the desert granivore system. – In: Diamond, J. and Case, T. J. (eds), *Community ecology*. Harper and Row, New York, pp. 41–61.
- Brown, J. H., Valone, T. J. and Curtin, C. G. 1997. Reorganization of an arid ecosystem in response to recent climate change. – *Proc. Natl. Acad. Sci. USA* 94: 9729–9733.
- Buckland, S. T., Anderson, D. R., Burnham, K. P. and Laake, J. L. 1993. Distance sampling, estimating abundance of biological populations. – Chapman and Hall, New York.
- Carpenter, S. R. and Kitchell, J. F. 1988. Consumer control of lake productivity. – *BioScience* 38: 764–769.
- Chapin, F. S., III and Shaver, G. R. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. – *Ecology* 66: 564–576.
- Chapin, F. S., III, Shaver, G. R., Giblin, A. E. et al. 1995. Responses of arctic tundra to experimental and observed changes in climate. – *Ecology* 76: 694–711.
- Chew, R. M. and Butterworth, B. B. 1964. Ecology of rodents in Indian Cove (Mojave Desert), Joshua Tree National Monument, California. – *J. Mammal.* 45: 203–225.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. – *Ecology* 42: 710–723.
- Davis, M. B. 1986. Climatic instability, time lags, and community disequilibrium. – In: Diamond, J. and Case, T. J. (eds), *Community ecology*. Harper and Row, New York, pp. 269–284.
- Ehrlich, P. R. and Birch, L. C. 1967. The “balance of nature” and “population control”. – *Am. Nat.* 101: 97–107.
- Estes, J. A. and Palmisano, J. F. 1974. Sea-otters: their role in structuring nearshore communities. – *Science* 185: 1058–1060.
- Grace, J. B. and Pugsek, B. H. 1998. On the use of path analysis and related procedures for the investigation of ecological problems. – *Am. Nat.* 152: 151–159.
- Graham, R. W. 1986. Response of mammal communities to environmental changes during the late Quaternary. – In:

- Diamond, J. and Case, T. J. (eds), Community ecology. Harper and Row, New York, pp. 300–313.
- Grant, P. R. and Grant, B. R. 1996. Finch communities in a climatically fluctuating environment. – In: Cody, M. L. and Smallwood, J. A. (eds), Long-term studies of vertebrate communities. Academic Press, San Diego, CA, pp. 343–384.
- Guo, Q. F. and Brown, J. H. 1996. Temporal fluctuations and experimental effects in desert plant-communities. – *Oecologia* 107: 568–577.
- Hafner, M. S. 1977. Density and diversity in Mojave desert rodent and shrub communities. – *J. Anim. Ecol.* 46: 925–938.
- Hairston, N. G., Smith, F. E. and Slobodkin, L. B. 1960. Community structure, population control and competition. – *Am. Nat.* 94: 421–425.
- Hanson, J. M. and Peters, R. H. 1984. Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. – *Can. J. Fish. Aquat. Sci.* 41: 439–445.
- Hastings, A., Hom, C. L., Ellner, S. et al. 1993. Chaos in ecology: is mother-nature a strange attractor. – *Annu. Rev. Ecol. Syst.* 24: 1–33.
- Heske, E. J., Brown, J. H. and Mistry, S. 1993. Long-term experimental study of a desert rodent community: 13 years of competition. – *Ecology* 75: 438–445.
- Hillel, D. and Tadmor, N. 1962. Water regime and vegetation in the central Negev highlands of Israel. – *Ecology* 43: 33–41.
- Hunter, M. D. and Price, P. W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. – *Ecology* 73: 724–732.
- Jaksic, F. M., Silva, S. I., Meserve, P. L. and Gutierrez, J. R. 1997. A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America. – *Oikos* 78: 341–354.
- Leibold, M. A. and Wilbur, H. M. 1992. Interactions between food-web structure and nutrients on pond organisms. – *Nature* 360: 341–343.
- Leibold, M. A., Chase, J. M., Shurin, J. B. and Downing, A. L. 1997. Species turnover and the regulation of trophic structure. – *Annu. Rev. Ecol. Syst.* 28: 467–494.
- Lima, M., Keymer, J. E. and Jaksic, F. M. 1999. El Niño–Southern oscillation-driven rainfall variability and delayed density dependence cause rodent outbreaks in Western South America: linking demography and population dynamics. – *Am. Nat.* 153: 476–491.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. – *Am. Nat.* 112: 23–39.
- McCauley, E. and Kalff, J. 1981. Empirical relationships between phytoplankton and zooplankton biomass in lakes. – *Can. J. Fish. Aquat. Sci.* 38: 458–463.
- McClelland, W. T. and Hain, F. P. 1979. Survival of declining *Dendroctonus frontalis* populations during a severe and nonsevere winter. – *Environ. Entomol.* 8: 231–235.
- McNaughton, S. J., Oesterheld, M., Frank, D. A. and Williams, K. J. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. – *Nature* 341: 142–144.
- Mehlman, D. W. 1997. Change in avian abundance across the geographic range in response to environmental change. – *Ecol. Appl.* 7: 614–624.
- Meserve, P. L., Yunker, J. A., Gutierrez, J. R., Yunker, J. A. 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. – *J. Mammal.* 76: 580–595.
- Meserve, P. L., Gutierrez, J. R. et al. 1996. Role of biotic interactions in a small mammal assemblage in semiarid Chile. – *Ecology* 77: 133–148.
- Mock, C. J. 1996. Climatic controls and spatial variation of precipitation in the western United States. – *J. Climate* 9: 1111–1125.
- Murdoch, W. W. 1966. Community structure, population control and competition – a critique. – *Am. Nat.* 100: 219–226.
- Oksanen, L. 1992. Evolution of exploitation ecosystems I. Predation, foraging ecology and population dynamics in herbivores. – *Evol. Ecol.* 6: 15–33.
- Oksanen, L., Fretwell, S. D., Arruda, J. and Niemelä, P. 1981. Exploitation ecosystems in gradients of primary productivity. – *Am. Nat.* 118: 240–261.
- Olsen, L. F. and Schaffer, W. M. 1990. Chaos versus noisy periodicity: alternative hypotheses for childhood epidemics. – *Science* 249: 499–504.
- Ostfeld, R. S. 1997. The ecology of Lyme-disease risk. – *Am. Sci.* 85: 338–346.
- Ostfeld, R. S., Canham, C. D. and Pugh, S. R. 1993. Intrinsic density-dependent regulation of vole populations. – *Nature* 366: 259–261.
- Paine, R. T. 1966. Food web complexity and species diversity. – *Am. Nat.* 100: 65–75.
- Parmenter, C. A., Yates, T. L., Parmenter, R. R. et al. 1998. Small mammal survival and trapability in mark-recapture monitoring programs for Hantavirus. – *J. Wildl. Dis.* 34: 1–12.
- Parmenter, R. R., Brunt, J. W., Moore, D. I. and Ernest, S. 1993. The Hantavirus epidemic in the Southwest: rodent population dynamics and the implications for the transmission of Hantavirus-associated Adult Respiratory Distress Syndrome (HARDS) in the Four Corners Region. – Report to the Federal Centers for Disease Control and Prevention, Atlanta, GA. Sevilleta LTER Publ. Ser. 41, pp. 1–45.
- Parmesan, C. 1996. Climate and species range. – *Nature* 382: 765–766.
- Pianka, E. R. 1986. Ecology and natural history of desert lizards. – Princeton Univ. Press, Princeton, NJ.
- Polis, G. A., Hurd, S. D., Jackson, C. T. and Sanchez-Pinero, F. 1998. Multifactor population limitation: variable spatial and temporal control of spiders on Gulf of California Islands. – *Ecology* 79: 490–502.
- Power, M. E. 1990. Effects of fish in river food webs. – *Science* 250: 811–814.
- Power, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy? – *Ecology* 73: 733–746.
- Power, M. E., Tilman, D., Estes, J. A. et al. 1996. Challenges in the quest for keystones. – *BioScience* 46: 609–620.
- Rice, W. R. 1990. A consensus combined p-value test and the family-wide significance of component tests. – *Biometrics* 46: 303–308.
- Rosenzweig, M. L. 1968. Net primary productivity of terrestrial environments: predictions from climatological data. – *Am. Nat.* 102: 67–84.
- Sala, O. E., Parton, W. J., Joyce, L. A. and Lauenroth, W. K. 1988. Primary production of the central grassland region of the United States. – *Ecology* 69: 40–45.
- Samson, D. A., Philippi, T. E. and Davidson, D. W. 1992. Granivory and competition as determinants of annual plant diversity in the Chihuahuan desert. – *Oikos* 65: 61–80.
- Schaffer, W. M. and Kot, M. 1985. Nearly one dimensional dynamics in an epidemic. – *J. Theor. Biol.* 112: 403–427.
- Schindler, D. W. 1977. Evolution of phosphorus limitation in lakes. – *Science* 195: 260–262.
- Slobodkin, L. B., Smith, F. E. and Hairston, N. G. 1967. Regulation in terrestrial ecosystems, and the implied balance of nature. – *Am. Nat.* 101: 109–124.
- Smith, F. A., Brown, J. H. and Valone, T. J. 1997. Path analysis: a critical evaluation using long-term experimental data. – *Am. Nat.* 149: 29–42.
- Smith, F. A., Brown, J. H. and Valone, T. J. 1998. Path modeling methods and ecological interactions: a response to Grace and Pugsek. – *Am. Nat.* 152: 160–161.

- Sutcliffe, O. L., Thomas, C. D. and Moss, D. 1996. Spatial synchrony and asynchrony in butterfly population dynamics. – *J. Anim. Ecol.* 65: 85–95.
- Swetnam, T. W. and Betancourt, J. L. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. – *J. Climate* 11: 3128–3147.
- Tevis, L., Jr. 1958a. Germination and growth of ephemerals induced by sprinkling a sandy desert. – *Ecology* 39: 681–688.
- Tevis, L., Jr. 1958b. A population of desert ephemerals germinated by less than one inch of rain. – *Ecology* 39: 688–695.
- Tilman, D. and Downing, J. A. 1994. Biodiversity and stability in grasslands. – *Nature* 367: 363–365.
- Turchin, P., Lorio, P. L., Jr., Taylor, A. D. and Billings, R. F. 1991. Why do populations of southern pine beetles (Coleoptera:Scolytidae) fluctuate? – *Environ. Entomol.* 20: 401–409.
- Valone, T. J. and Brown, J. H. 1996. Desert rodents: long-term responses to natural changes and experimental manipulations. – In: Cody, M. L. and Smallwood, J. A. (eds), *Long-term studies of vertebrate communities*. Academic Press, San Diego, CA, pp. 555–583.
- Vanni, M. J. 1987. Effects of nutrients and zooplankton size on the structure of a phytoplankton community. – *Ecology* 68: 624–635.
- Vanni, M. J., Luecke, C., Kitchell, J. F. et al. 1990. Effects on lower trophic levels of massive fish mortality. – *Nature* 344: 333–335.
- Whitford, W. G. 1976. Temporal fluctuations in density and diversity of desert rodent populations. – *J. Mammal.* 57: 351–369.