

Rain and Rodents: Complex Dynamics of Desert Consumers

JAMES H. BROWN AND S. K. MORGAN ERNEST

Water is the lifeblood of the desert. It comes in rains that are typically scant and sporadic, but can be so intense as to cause flooding. Because water is the resource in shortest supply, the amount and timing of precipitation directly limits plant growth and primary production. Seasons of exceptionally heavy and frequent rains produce the spectacular desert blooms shown in nature films and magazines. Seasons of exceptionally high rainfall are also thought to cause increases in rodent populations and outbreaks of rodent-borne diseases such as hantavirus and plague. El Niño is supposed to cause exceptionally heavy winter rainfall in the deserts of southwestern North America, leading in turn to plant growth, abundant seeds and insects, high populations of small mammals, density-dependent increases in parasites and diseases, and increased contact between rodents, their pathogens, and humans, resulting in disease epidemics. Thus, the outbreak of the Sin Nombre strain of hantavirus that killed 27 people in the Four Corners region of the southwestern United States in the summer of 1993 was attributed to the rains, plant production, and rodent increases triggered by the El Niño events of 1991–1992 and 1992–1993 (Harper and Meyer 1999).

Ecologists have long been interested in these kinds of complicated pathways of interactions and particularly in how relationships between resources and consumers affect the structure and dynamics of ecosystems. The “bottom-up” pattern of regulation described above occurs when pulsatile resource inputs are transmitted up food chains, causing increases first in plants and then in successively higher trophic levels. This contrasts with “top-down” regulation, in which the feeding activities of top carnivores cascade down food chains to affect successively lower trophic levels (e.g., Hairston et al. 1960, Oksanen et al. 1981, Carpenter and Kitchell 1988). But ecological systems are complex, and there is reason to believe that resource–consumer relationships can exhibit chaotic or other forms of complicated nonlinear dynamics (e.g., Schaffer and Kot 1985, Hanski et al. 1993, Hastings et al. 1993, Lima et al. 1999).

ALTHOUGH WATER IS THE PRIMARY LIMITING RESOURCE IN DESERT ECOSYSTEMS, THE RELATIONSHIP BETWEEN RODENT POPULATION DYNAMICS AND PRECIPITATION IS COMPLEX AND NONLINEAR

Long-term ecological studies provide unique opportunities to study resource–consumer relationships in realistically complex natural settings. Since 1977 we have been monitoring the weather, plants, and rodents in the Chihuahuan Desert near Portal, Arizona (figure 1; Brown 1998, Ernest et al. 2000). The resulting data allow us to evaluate the relationship between El Niño events and rainfall, the dependence of plants on precipitation, and the ways in which episodic rains affect desert rodent populations. After 23 years of study, we are far from understanding the dynamics of this ecosystem. One thing that is clear, however, is that simple bottom-up regulation does not occur. The responses of desert consumers to precipitation are complex and nonlinear.

The simple model

Figure 2 depicts a qualitative model for water resource regulation of desert rodent populations. Precipitation leads to germination, growth, and reproduction of plants, and the resulting increases in food supply in the form of seeds, fruits, and leaves lead to increases in rodent populations. The model assumes simple trophic transmission of pulses of resources

James H. Brown (e-mail: jhbrown@unm.edu) is a Regents' Professor, and S. K. Morgan Ernest (e-mail: mernest@unm.edu) is a PhD student, in the Department of Biology, University of New Mexico, Albuquerque, NM 87131. They use data from Brown's long-term field study in the Chihuahuan Desert to pursue their interests in the structure and dynamics of ecological communities.
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Figure 1. Photograph of our long-term research in the Chihuahuan Desert near Portal, Arizona, where we have been collecting data on precipitation, plants, and rodents since 1977.

from precipitation on to plants to herbivores and, by implication, on upward through carnivores and higher trophic levels. According to this model, a cause-and-effect chain of resource limitation is transmitted up the trophic chain. If this model is correct, then at each trophic level, after an appropriate time lag, fluctuations in population should vary directly with fluctuations in available water caused by precipitation events.

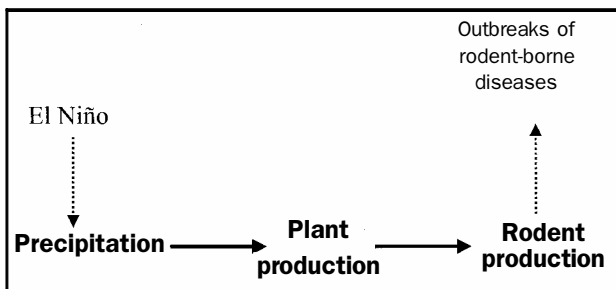


Figure 2. A simple linear model showing how pulses in resource availability are thought to be transmitted with time lags up food chains to affect successively higher trophic levels. This figure shows in boldface type the postulated effect of precipitation on plant production and of plant food resources on rodent populations. The postulated effects of El Niño on precipitation and of rodent populations on hantavirus are shown in a lighter typeface.

This simple model is not without theoretical foundation or empirical support. Water is the primary limiting resource for desert plants, so it would seem logical that the quantity and timing of germination, growth, and reproduction would be closely tied to precipitation events. Since most desert rodents obtain nearly all their food and water from plants, it would seem equally logical that fluctuations in rodent populations would be closely tied to variation in plant production, and therefore also to variation in precipitation. Indeed, this simple model does seem to work well some of the time, at certain spatial and temporal scales. Data from geographic comparisons across large spatial scales, as well as from some short-term observations, provide strong evidence for dynamic linkages from precipitation through plants to rodent populations.

Support for the model: Comparative geographic studies

One kind of evidence comes from patterns of rodent abundance, distribution, and diversity in geographic gradients of varying precipitation. Comparative studies of rodents from small patches of relatively uniform habitat across the southwestern United States reveal clear trends. These studies have used standardized methods to census rodents in habitats of comparable soil type and vegetation structure, thereby holding constant habitat variables that are known to affect rodent

ecology (Rosenzweig and Winakur 1969, Rosenzweig 1973, Brown 1975, M'Closkey 1978, Price 1978, Brown et al. 1979, Kotler and Brown 1988, Price and Podolsky 1989). The most arid parts of the Mojave and Colorado Deserts receive on average about 100 millimeters (mm) of precipitation per year, and typical habitats support low populations of only one or two granivorous rodent species. As precipitation increases in geographic gradients to the east and north, there are strong trends of increasing rodent species richness and overall rodent abundance. There are two pronounced peaks, one in the transition between the Sonoran and Chihuahuan Deserts in southeastern Arizona and southwestern New Mexico, and the other in the Great Basin Desert of northwestern Nevada. In these regions, which receive 52 to 321 mm of annual precipitation, it is not uncommon to find 5 to 10 species coexisting in shrubby habitats with sandy soils. So, along these gradients, both rodent species richness and total rodent abundance are correlated with mean annual precipitation (figure 3; Brown 1973, 1975, Brown and Harney 1993, Shenbrot et al. 1994).

These geographic patterns undoubtedly reflect the role of precipitation in limiting producers and consumers in arid regions. Rosenzweig (1968; see also Hillel and Tadmor 1962) showed that long-term average primary production in arid regions is closely correlated with average precipitation and actual evapotranspiration, and there is abundant evidence that seed production is correlated with primary production and precipitation. There is also considerable information on how rodent abundance and species diversity are influenced by food resources. With increasing precipitation and food availability, rodents become more specialized for particular food types and microhabitats, resulting in more complete and efficient exploitation of the food resources by a greater number of individuals and species (Brown and Lieberman 1973, Brown 1975, M'Closkey 1976, Shenbrot et al. 1994, Kelt et al. 1996).

There is also evidence from these geographic studies that rodent population dynamics and community structure are affected by factors in addition to precipitation and food availability. Nearby habitats with nearly identical precipitation can differ markedly in rodent abundance and species composition. Often these differences appear to reflect variation in risk of predation (Rosenzweig and Winakur 1969, Rosenzweig 1973, Price 1978, Thompson 1982, Kotler 1984, Kotler and

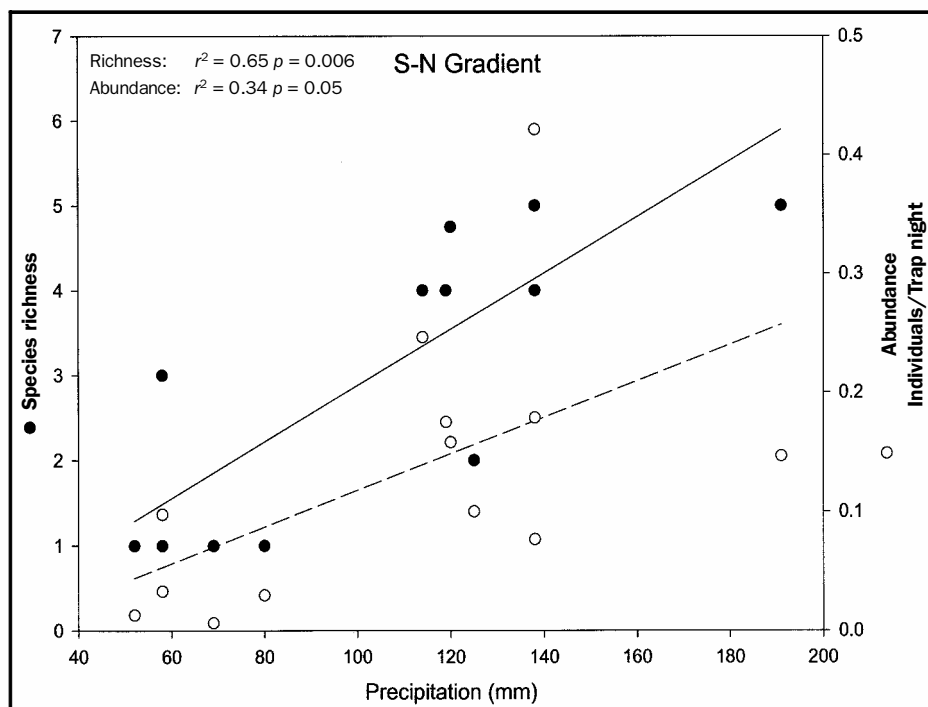


Figure 3. Relation between number of rodent species, total rodent abundance, and mean annual precipitation along a south–north gradient of increasing rainfall from the Colorado and Mojave Deserts of southern California to the Great Basin Desert of northwestern Nevada. Both number of species and overall abundance of rodents increase with increasing precipitation. From data in Brown (1973).

Brown 1988, Brown 1989). This raises the possibility that rodent populations are regulated not only from the bottom up by resource availability but also from the top down by predation.

Support for the model: Short-term studies

Short-term studies of rodent populations and community dynamics also appear to support the simple model of bottom-up regulation of desert rodent populations arising from fluctuations in precipitation and food resources. We can divide these studies into three groups. The first group documents rodent responses to single- or one-season rainfall events. Most of these studies have taken advantage of opportunities to study the consequences of rare, extreme precipitation regimes in extremely arid ecosystems. Their almost universal observation was that drought-breaking precipitation was followed by increases in rodent populations, and that extreme precipitation events—either single episodes of exceptionally heavy rainfall or entire seasons of far-above-average precipitation—were followed by exceptionally high rodent populations. A classic example is Beatley's (1967, 1969) documentation of plant and rodent responses to a single rainfall event in the northern Mohave Desert, but several other studies (e.g., Reynolds 1958, French et al. 1974, O'Farrell et al. 1975, Whitford 1976, Meserve et al. 1995) fall into this first group.

The second group of studies documents longer-term correlations between precipitation inputs and rodent responses. Some of these studies also provide evidence for the intermediary link, that is, some kind of plant response such as increased productivity or cover following high rainfall. For example, Ernest and colleagues (2000) recently documented the relationship between precipitation, plant production, and rodent populations over an 8-year period at the Sevilleta Long-Term Ecological Research (LTER) site in central New Mexico. In general, this study found positive correlations, with successive time lags, among three variables—total seasonal precipitation, plant cover, and total abundance of all rodent species—in five habitats ranging from desert shrubland through arid grassland to juniper woodland. Differences in summer rainfall patterns among habitats were reflected in differences in plant responses and rodent populations. Other studies in this second group are by Petryszyn (1982), Brown and Heske (1990), Brown and Harney (1993), and Madsen and Shine (1999).

The third group of studies focuses on the apparent influence of precipitation associated with El Niño events or with the El Niño–Southern Oscillation (ENSO) pattern. The last decade has seen considerable progress in understanding the linkages between oceanographic events and climate, especially those linkages between changes in currents in the eastern Pacific and shifts in climate in the western regions of both North and South America. The ENSO phenomenon has been linked to changing patterns of precipitation and related ecological dynamics in the southwestern United States and other arid regions, such as northern Chile. Several studies have reported increases in desert rodent populations following single or multiple El Niño events. Brown and Heske (1990) pointed out that three peaks in rodent populations at Brown's long-term study site between 1977 and 1987 appeared to be associated with higher-than-normal winter precipitation coinciding with the three El Niño events that occurred during that period. Similarly, Meserve and colleagues (1995) reported a large increase in rodents at their long-term research site in coastal Chile following the El Niño event of 1991–1992.

These relatively short-term studies have encouraged widespread promulgation and acceptance of the simple model for the bottom-up influence of precipitation on rodents and other consumers in arid ecosystems. This model has been widely applied not only to account for the dynamics of desert rodent populations but also to explain how outbreaks of hantavirus and peaks of predator populations can be related to the trophic chain extending from precipitation through plants and mammalian herbivores to higher trophic levels (Jakšic et al. 1997, Polis et al. 1998).

Failure of the model: Long-term studies and complex dynamics

Compilation and analysis of data from our long-term studies near Portal, Arizona, in the Chihuahuan Desert suggest that the simple bottom-up trophic model is too simplistic. At least at our site, population and community dynamics of

desert rodents are complex and nonlinear (“nonlinear” refers simply to the lack of a consistent monotonic relationship). At Portal, fluctuations in rodent populations cannot be explained simply in terms of pulses of limiting resources being passed with successive time lags up trophic chains following precipitation events. We illustrate this point by describing three results from Portal and considering their broader implications.

The first result is that the apparent relationship between El Niño events and peaks in rodent abundance that we observed in the 1970s and 1980s failed to hold in the 1990s (figure 4). There were two El Niño events in the 1990s: a double El Niño in 1991–1992 and 1992–1993 and a single, very strong El Niño in 1997–1998. Neither was followed by an increase in rodent abundance. In fact, rodents reached near all-time low numbers during and after the double 1991–1992 and 1992–1993 event. Furthermore, after near-record lows in the mid-1990s, rodents reached near-record high numbers in the summer of 1997, but this peak was not associated with an El Niño event.

It is important to mention that the 1997–1998 El Niño did not result in unusually high winter precipitation at the study site. In this El Niño, which was estimated to be the strongest one in the 20th century, warm sea surface temperatures extended far to the north along the Pacific coast, and although the El Niño did cause exceptionally heavy winter precipitation, most of the storms tracked well to the north of our study site. This observation suggests that El Niño is itself a complex phenomenon, and there may be no simple relationship between ENSO, sea surface temperature in the northeastern Pacific, and winter precipitation in the southwestern United States.

Similar results have come from Chile, where a short-term study had documented peaks in populations of rodents, especially the dominant species *Octodon degu*, following El Niño (Meserve et al. 1999). However, longer-term records and comparisons across sites revealed that El Niños were not invariably followed by increases in degu populations (Lima et al. 1999). In fact, spatially separated populations showed dynamics that were out of phase with each other and often out of phase with ENSO. This observation led Lima and colleagues (1999) to propose that degu populations exhibit chaotic dynamics.

The second result is that 23 years of data from Portal clearly show there has been no simple relationship between precipitation input, plant responses, and rodent population increases. There was indeed a positive correlation between abundance of annual plants and total seasonal precipitation, but rodent abundance was not correlated with either the quantity of precipitation or the abundance of plants (Ernest et al. 2000). When we began the Portal study, we believed that with a sufficiently long time series of data, it would be possible to document clear relationships between the temporal pattern of precipitation and drought, variation in plant growth and seed production, and rodent population fluctuations. As the length of the time series has grown, however, the relationships have become less rather than more clear. In-

deed, the magnitude of the correlation between seasonal precipitation and lagged rodent abundance, rather than increasing or at least stabilizing with increasing time, actually appears to decrease (figure 5).

Some possible reasons for this finding, and for the lack of a consistent response to El Niño, come from analysis of shorter time series from the Sevilleta LTER site, located at the northern edge of the Chihuahuan Desert about 300 kilometers (km) northeast of Portal. These time series do show positive correlations with appropriate lags between seasonal precipitation, plant cover, and rodent populations (Ernest et al. 2000). They also show that sites less than 30 km apart can have very different patterns of precipitation, plant response, and rodent dynamics, apparently because of differences in summer precipitation. Winter precipitation, including that associated with El Niño, comes from frontal storm systems that originate over the Pacific Ocean and then travel eastward across the southwestern United States. Summer precipitation comes from intense thunderstorms, which are highly localized but strongly influenced by mountains and other topographic features. Ernest and colleagues (2000) showed that the dynamics of plants and rodents are strongly influenced by summer as well as winter precipitation and that correlations between precipitation, plants, and rodents cannot be detected unless the localized nature of summer precipitation is taken into account. Because close to 60% of the yearly precipitation at both the Sevilleta and Portal sites can be attributed to summer storms, the high spatial and temporal variability of these localized cells can decouple the rodent and plant dynamics of sites only a few kilometers apart. In contrast, there are no strong responses that can be attributed to El Niño events alone. While these observations at Sevilleta reveal some of the complications involved in explaining variation in plant and rodent responses to patterns of precipitation, they are not much help in understanding the more complex dynamics at Portal. A weather station monitors local rainfall at Portal, and we know that the plants, but not the

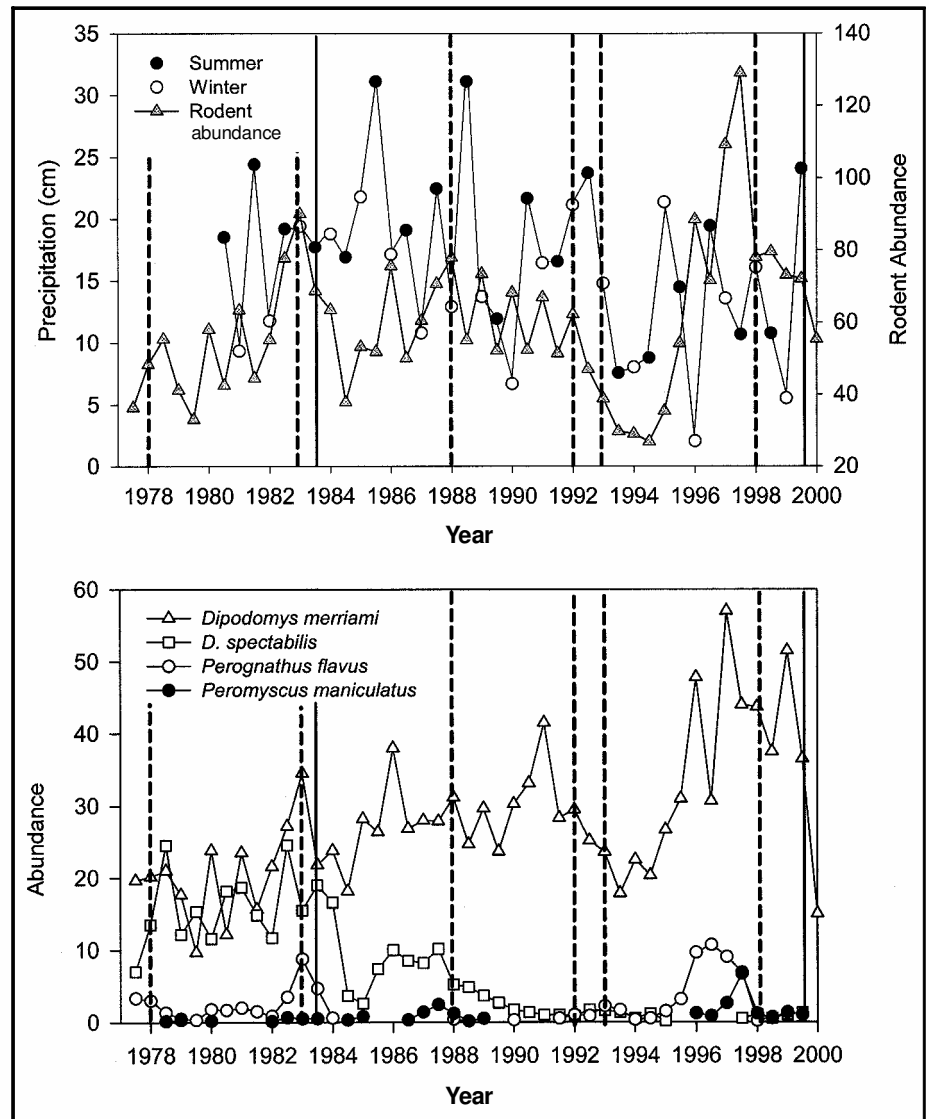


Figure 4. Temporal dynamics of rainfall and rodent populations at our long-term study site in southeastern Arizona since 1977. Shown in the top panel are winter and summer precipitation (open and closed circles, respectively) and total abundance of all rodents in a 6-month period (gray triangles). In the bottom panel are populations of four rodent species: two kangaroo rats (*Dipodomys spectabilis* and *D. merriami*), a pocket mouse (*Perognathus flavus*), and the deer mouse (*Peromyscus maniculatus*). Also shown in both are the six El Niño events (1977–1978, 1982–1983, 1987–1988, 1991–1992, 1992–1993, and 1997–1998; bold dashed lines) and two extreme rainfall events (Tropical Storm Octave in fall 1983 and an intense thunderstorm in summer 1999; narrow black lines) that occurred during this period. Note that there is no consistent relationship between rodent populations and rainfall or El Niño events, but the two extreme rainfall events caused catastrophic decreases in rodents, of *D. spectabilis* and *P. flavus* in 1983 after Tropical Storm Octave and of *D. merriami* in 1999 after the flooding caused by the thunderstorm.

rodents, showed consistent responses to seasonal precipitation.

The third result may help to explain why rodents failed to respond to precipitation events that caused peaks in plant production at Portal. It is increasingly clear that there is not a simple set of more or less linear relationships between precipi-

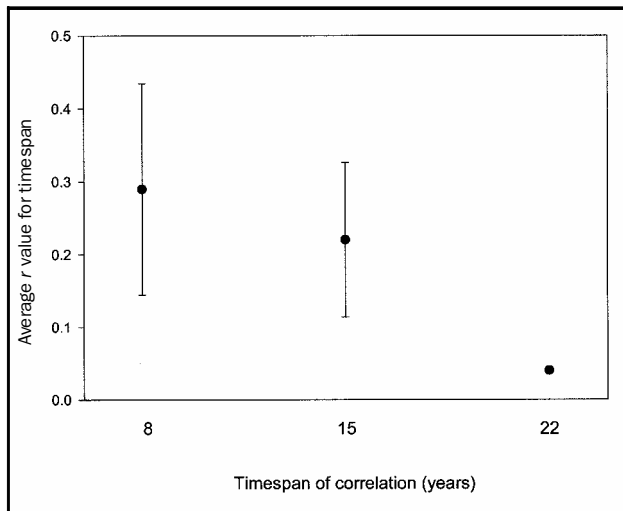


Figure 5. Average correlation coefficients and standard deviations for relationships between total rodent abundance and mean precipitation for 6-month periods at the long-term site in southeastern Arizona for three windows of increasing time duration: 8 years, 15 years, and 22 years. Correlations were calculated on all possible 8-, 15-, and 22-year segments in the data set and then averaged. Note that the correlation for the entire time span is actually lower than for shorter periods, rather than increasing with increasing length of the time series, as would be expected if the relationship between precipitation and rodent abundance were consistent.

tation inputs, plant production, and rodent population fluctuations. The rodent responses are complex and nonlinear. They depend on the temporal pattern, as well as the total quantity, of seasonal precipitation and probably on other factors, such as the abundance of predators. Unfortunately, we have not had sufficient resources to monitor the predators of rodents at Portal.

We can, however, show that the response of rodents to precipitation has a nonlinear component. Extremely heavy rainfall can actually cause decreases in rodent populations. Obviously, this is in stark contrast to the increases that would be predicted if the effects of precipitation are mediated through plant production and food availability. Figure 4 shows the fluctuations in the abundances of the two rodent species that were most abundant at Portal when we started our study in 1977. Note that the second most abundant species, the banner-tailed kangaroo rat, *Dipodomys spectabilis*, showed a catastrophic decline over the winter of 1983–1984. This crash followed Tropical Storm Octave, which, during a 6-day period (27 September–3 October 1983), deposited 129 mm of precipitation, nearly half the annual average for the study site (Valone et al. 1995). The decline in *D. spectabilis* can probably be attributed to the fact that this kangaroo rat stores seeds in large granaries (Vorhies and Taylor 1922, Monson 1943), and its food stores were wetted and spoiled. Another rodent species, the pocket mouse *Perognathus flavus*, and several species of harvester ants, all of which store seeds in underground larders,

crashed at the same time. (Please note that other factors must be invoked to account for the failure of *D. spectabilis* to recover following this event [see Valone et al. 1995].)

Figure 4 shows that Merriam's kangaroo rat (*D. merriami*), consistently the most abundant rodent species on the study site, crashed in late 1999. We know with certainty that this was due to a single intense thunderstorm that deposited more than 30 mm of rain in a period of less than 2 hours on 14 August 1999. This storm caused sheet flooding over the whole site to a depth of nearly 35 centimeters. Although kangaroo rats show a good basic ability to locomote in water by swimming, in the same way that other terrestrial mammals are able to swim (G. J. Kenagy, University of Washington, Seattle, personal communication, 2002), they were apparently unable to rescue themselves from the torrential flood that occurred. (We note parenthetically that the flood killed the lone individual of *D. spectabilis* and the few individuals of a third kangaroo species, *D. ordii*, that were present on the site. *D. merriami* was only minimally affected by Tropical Storm Octave, because it does not store seeds in underground larders and the rainfall was spread over a sufficient period that there was no surface flooding.) These observations point out one reason for the lack of consistent relationships over the long term between seasonal precipitation patterns, plant production, and rodent population dynamics. Because extreme precipitation events can either cause catastrophic declines in rodent populations or stimulate population increases through increased food supply, the nonlinear effects of extreme infrequent events preclude any consistent statistical relationship between precipitation, plant productivity, and rodent abundance.

There is reason to believe that there are other nonlinear relationships that further complicate the relationships between desert rodents and their resources. It is likely that predators play a role. We know that, at least sometimes, populations of mammalian, avian, and reptilian predators increase in response to population peaks in their rodent prey. It is easy to imagine that if seasons of high rainfall and plant production occur sufficiently close together, high predator populations that have built up in response to the first favorable season could inhibit or even prevent a rodent increase in response to the second favorable season. On the other hand, if favorable seasons are separated by sufficient time, so predators that may have increased will have declined again, then the rodent populations could increase relatively unchecked by predators. Unfortunately, data to document such a nonlinear effect of predators are limited, and, in the case of Portal, nonexistent. However, Lima and colleagues (1999) invoke just this kind of nonlinear effect of predators to explain the apparently chaotic dynamics of rodent populations in response to ENSO events in Chile. It is likely that parasites, diseases, and other biotic and abiotic factors could also have nonlinear effects, complicating or obscuring any straightforward effect of precipitation on rodents or other consumers.

General implications

We have restricted our consideration to desert rodents, because our long-term data allow us to speak with some authority. Nevertheless, we believe that many of the lessons learned from rodents are applicable to other kinds of organisms.

Over the last several decades we have seen a simple paradigm for the bottom-up influence of precipitation on desert rodents be put forward, receive initial support, and ultimately be proved inadequate. There are some valuable lessons here. First, the simple model is not really wrong; it is just too simplistic to capture the complex dynamics of desert ecosystems. While deserts may seem simple—and may indeed be relatively simple compared with systems such as tropical rain forests—they are actually richly and challengingly complex. The mechanistic processes invoked in the simple model are undoubtedly correct: The availability of water affects many aspects of the structure and dynamics of arid ecosystems; the temporal pattern of precipitation and drought influences primary productivity and seed production; and the availability of seeds and other plant resources affects populations of herbivores, including seed-eating rodents. But other factors play important roles: Plant responses to precipitation depend not just on the total quantity of rainfall within a season but also on the magnitude and timing of individual rainfall events and on other abiotic factors (such as temperature) and biotic interactions (such as herbivory); and fluctuations in rodent populations depend not only on availability of food resources but also on other factors, both abiotic and biotic, such as extreme weather events and predators.

The result is that no simple linear model is likely to be able to capture realistically the large number of environmental variables and ecological processes that affect population dynamics. This is true for a single species population and also for total abundance of all species within a guild or functional group, such as rodents. Furthermore, there is no reason to believe that such complex interactions and nonlinear dynamics should be confined to a particular guild, functional group, or trophic level. We might expect that responses of plants to precipitation would be simpler and more predictable than those of higher trophic levels, and some of our data from Portal would support this hypothesis. Yet even the plants exhibit complex dynamics. In the winter of 1998–1999, there were heavy early rains at Portal, and many annuals germinated. There was virtually no precipitation during the remainder of the season, however, and nearly all of the annuals died without setting seed. Any model that would accurately account for plant responses to precipitation must include the timing as well as the magnitude of rainfall events.

Since the simple models are inadequate, it will be difficult to predict the structure and dynamics of these systems. While it may be possible in some cases to understand the causes of fluctuations after they have happened, it will be almost impossible to predict the behavior of the system in the future. The effects of extreme rainfall events on the kangaroo rats illustrate this point.

There are important practical implications. The Sin Nombre strain of hantavirus, which caused many human deaths in the Four Corners region of the southwestern United States in the early 1990s, is maintained in reservoir populations of rodents. The current model for the outbreak of hantavirus is a modification of the bottom-up trophic model for the influence of precipitation on rodents. According to this model, (a) El Niño events cause exceptionally heavy winter precipitation; (b) high precipitation causes peaks in plant growth and seed production; (c) high food availability causes increases in seed-eating rodent populations; (d) high abundance of rodent species and frequent contacts among individuals facilitate hantavirus transmission, leading to high infection rates in rodent populations; (e) high populations bring increased numbers of infected rodents into proximity with humans; and (f) contact with urine and feces of infected rodents causes transmission of hantavirus to humans (Parmenter et al. 1993, Mills et al. 1999). This model was based on one sequence of the above events that occurred following the 1991–1992 and 1992–1993 El Niños. The failure to observe high levels of hantavirus in either rodents or humans in the Four Corners region following the 1997–1998 El Niño suggests that the simple linear bottom-up model is too simplistic. Additional evidence comes from the failure to observe any consistent relationship between El Niño events and rodent populations at Portal—including populations of the deer mouse, which appears to be the primary reservoir for the Sin Nombre strain of hantavirus (figure 4).

We have similar concerns about other studies that imply that outbreaks of rodent-borne diseases can be predicted from simple linear cause-and-effect models of limiting factors transmitted through chains of ecological interactions. One example is Lyme disease in the northeastern United States. Recent studies trace fluctuations in human infections of Lyme disease to a chain of ecological interactions extending from climate through production of acorns and other mast crops to increases in reservoir white-footed mouse (*Peromyscus leucopus*) populations and then through tick vectors to humans (Ostfeld et al. 1996, Jones et al. 1998). In the cases of hantavirus, plague, Lyme disease, and other rodent-borne diseases, we do not question the sequence of events that has been observed or the mechanistic interactions that have been invoked to explain them. We do believe, however, that the lessons of the complex relationships between precipitation and rodent population dynamics from Portal and Chile provide good reason to question the predictive power of simple linear models. These long-term studies suggest that many confounding variables and contingent events can affect the fidelity and dynamics of transmission of pulsatile signals through chains of ecological interactions. Shorter-term studies may allow identification of important mechanisms, but they may be inadequate to reveal the complexities of the dynamics. Researchers should make efforts to obtain long-term data to evaluate models, and they should observe caution in making predictions.

None of what we have presented in this article should be taken as challenging the view that water is the primary limiting resource that determines the structure and dynamics of arid ecosystems. This is true; it is almost tautological. But the very reason that water plays such a large role in arid ecosystems—the supply of water is determined by precipitation events occurring as sporadic pulses of widely varying magnitude and frequency—causes it to have complex nonlinear effects on the components of desert ecosystems. Results from our long-term studies do imply, however, that much additional research will be needed to understand the causes and consequences of water limitation in arid ecosystems. If we are ever to predict accurately the responses of desert plants and rodents to temporal and spatial variation in rainfall, a much better knowledge of the nonlinear relationships will be required. Since outbreaks of rodent-borne diseases are even more separated from the pulses of precipitation, both in the chain of ecological interactions and in time, to understand and predict these epidemics will be an even greater challenge.

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