BioOne COMPLETE

Responses of a Heteromyid Rodent Community to Large- and Small-scale Resource Pulses: Diversity, Abundance, and Home-range Dynamics

Authors: Orland, Mary C., and Kelt, Douglas A.

Source: Journal of Mammalogy, 88(5) : 1280-1287

Published By: American Society of Mammalogists

URL: https://doi.org/10.1644/06-MAMM-A-408.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Journal-of-Mammalogy on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Journal of Mammalogy, 88(5):1280–1287, 2007

RESPONSES OF A HETEROMYID RODENT COMMUNITY TO LARGE- AND SMALL-SCALE RESOURCE PULSES: DIVERSITY, ABUNDANCE, AND HOME-RANGE DYNAMICS

MARY C. ORLAND* AND DOUGLAS A. KELT

Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, 1 Shields Avenue, Davis, CA 95616, USA

We augmented food resources to a heteromyid rodent community in the Sonoran Desert of southern California to experimentally ascertain the effect of a resource pulse on rodent abundance, diversity, and home-range dynamics. The same community displayed increased rodent abundance and species diversity in response to the productivity pulse that resulted from the 1997–1998 El Niño Southern Oscillation (ENSO). In marked contrast to the response to the ENSO, our experiment resulted in a decline in rodent diversity because the largest pocket mouse present (*Chaetodipus formosus*) monopolized the added resources and increased its proportional abundance. In addition, the abundance of adult rodents did not change in response to supplemental resources, even though reproduction, and consequently juvenile abundance, increased greatly. This implies that home-range size and overlap by adult animals remained unchanged despite the greater abundance of food. Among caching species such as pocket mice, this may be an adaptive response to the highly variable and scarce resources of the desert environment. The decline in diversity and lack of change in adult density and home-range dynamics observed with the experimental resource pulse are directly counter to the response of the community to the ENSO resource pulse, and were apparently the result of fine-scale spatial processes. This suggests that the effects of resource pulses are scale-dependent, and that the results of small-scale manipulative experiments may provide limited insight into community responses to large-scale climatic events.

Key words: biodiversity, *Chaetodipus formosus*, coexistence, El Niño, environmental variability, productivity, Sonoran Desert, spatial scale, territoriality

Rainfall is a limiting factor for most mammals in arid systems. In North American deserts rainfall is positively correlated with primary productivity (LeHouerou et al. 1988; Whitford 2002) and with local small mammal species richness (Brown 1973; Brown et al. 1997). At larger spatial scales the relationship between small mammal richness and annual precipitation appears modal, with lower numbers at both low and very high values of precipitation (Brown 1995; Owen 1988; Reed et al. 2006). The resource heterogeneity hypothesis (Tilman 1982) states that at higher levels of resource availability, a species that is particularly effective at using this resource should become dominant and reduce the availability of these resources to other species. Recent work on mammals implicates such simple factors as structural barriers created by the growth of more lush vegetation at higher resource levels, and suggests that the underlying mechanism may differentially influence different trophic groups (Reed et al. 2006). Specifically, across a broad desert–grassland ecotone, granivorous rodents reached highest local richness at relatively low values for annual precipitation, whereas omnivores appeared to peak at high values of annual precipitation. Insectivorous species showed no clear relationship, and herbivores (perhaps predictably) increased with annual precipitation, likely reflecting increased forage.

At local spatial scales, however, little work has addressed responses of small mammal assemblages to precipitation. Valone et al. (1995) reported a catastrophic decline of *Dipodomys spectabilis* that evidently was in response to heavy winter rains, and Brown et al. (1997) documented major changes to local assemblage structure in response to elevated rainfall over nearly 3 decades. In Australia (Letnic et al. 2005) and northern Chile (Meserve et al. 2003) mammal communities respond dramatically to elevated rainfall associated with El Niño Southern Oscillation (ENSO—Holmgren et al. 2006a, 2006b). In addition to these demographic changes, theory and empirical data support arguments for behavioral responses to precipitation as well. For example, home range in mammals may vary

* *Correspondent: mcorland@ucdavis.edu*

© 2007 American Society of Mammalogists
www.mammalogy.org

Downloaded From: https://bioone.org/journals/Journal-of-Mammalogy on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

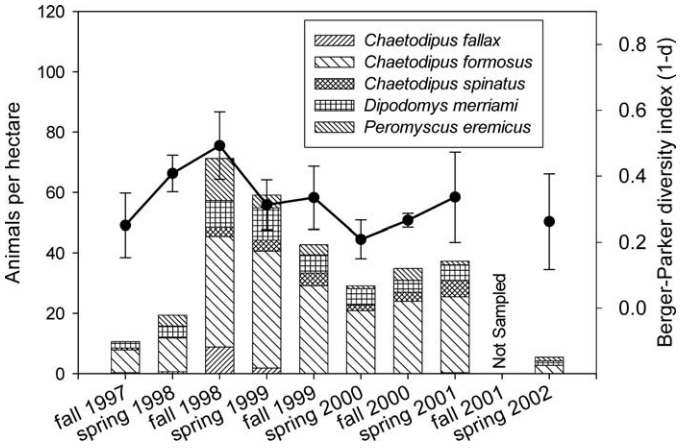


FIG. 1.—Mean rodent density by species, and Berger–Parker index ($1 - d$) for 4 monitoring sites, at Deep Canyon from 1997 to 2002. Species abbreviations are CHFA (*Chaetodipus fallax*), CHFO (*C. formosus*), CHSP (*C. spinatus*), DIME (*Dipodomys merriami*), and PEER (*Peromyscus eremicus*). Total abundance and diversity appeared to increase after the high productivity of the 1997–1998 El Niño Southern Oscillation event. Note the presence of the rare *C. fallax* in fall 1998 and spring 1999, suggesting that diversity may increase after a resource pulse.

within species as a function of resource availability (e.g., Boutin 1990; Oehler et al. 2003; but see, e.g., Relyea et al. [2000] and Vlasman and Fryxell [2002] for counterexamples).

We have been monitoring the small mammal community at a series of permanent livetrapping grids in the western Sonoran Desert of southern California since the mid-1990s. The small mammal community at this site responded dramatically to the 1997–1998 ENSO event (Fig. 1). Total rodent numbers increased markedly, and with this we documented increases in species richness, including both increases in the proportional abundance of the rarer species and in the immigration of a species normally found in slightly more productive, higher-altitude environments (Kelt 1999). The increased adult densities suggested a concomitant decrease in average home-range size, an increase in home-range overlap among the adult rodents, or both.

To better characterize rodent responses to resource availability we performed a resource supplementation experiment in 1999–2000. Our objective was to simulate the resource pulse to this community in the 1997–1998 ENSO. Results of our experimental study were very different from the natural experiment provided by the ENSO event, however, and explaining this discrepancy forced us to consider how regional and local resource pulses were experienced by the local assemblage. In retrospect this difference is not highly surprising, but it has provided additional insights to the importance of spatial scale, the role of manipulative field studies, and on the danger of extrapolating across scales. Our study thereby contributes to the larger ecological debate on ecological responses to resource pulses, while also yielding specific insight into the spatial dynamics and behavior of heteromyid rodents in response to resource pulses.

In summary, we designed our experiment to address the following questions. First, will species richness respond to an experimental resource pulse as it did to the regional pulse provided by ENSO, or alternatively, will richness decline as is commonly seen in resource-augmentation experiments? Second, will home-range size decrease or will home-range overlapp increase, or both, as seen during the resource pulse of the ENSO and in the majority of vertebrate species in resource-augmentation experiments, or will they remain unchanged as might be expected for a species in a harsh and highly variable environment? Although we did not monitor movements or otherwise quantify home-range size, we address this question indirectly by recording population density on plots of fixed area. Finally, can a small-scale experimental resource pulse successfully simulate a climatically induced resource pulse (i.e., are these dynamics scale-transcendent?), or alternatively, are assemblage dynamics scale-dependent where ''issues of scale'' prevent the direct application of experimental results to large-scale processes?

MATERIALS AND METHODS

Study area and species.—Both our resource pulse experiment and the long-term study were performed at the Philip L. Boyd Deep Canyon Desert Research Center (''Deep Canyon''; 33°38′10″N, 116°22′30″W) in the Coachella Valley near Palm Desert, California. As is typical for the Colorado Province of the Sonoran Desert, most rain at Deep Canyon falls in the winter and spring months in a small number of storms, averaging 145 mm/year. There is much interannual variation in this rainfall pattern, which has ranged from 27 to 478 mm/year since 1961 (M. Fisher, pers. comm.). Total rainfall from July 1997 to July 1998 was 297 mm, more than twice the long-term mean of 145 mm and reflecting the influence of the ENSO event in 1997–1998. Our study spanned the following 2 years, which experienced relatively low precipitation (49 mm and 59 mm, respectively), so our resource pulses occurred during a period of relatively low productivity. The dominant plant species in the study plots (see Zabriskie 1979) is creosote bush (*Larrea tridentata*), and the site also contains various species of cholla (e.g., *Opuntia basilaris*, *O. bigelovii*, and *O. ramosissima*) and barrel cacti (*Ferocactus cylindraceus* [= *F. acanthodes*]), with occasional desert shrubs (e.g., *Ambrosia dumosa*, *Psorothamnus schottii*, *Simmondsia chinensis*, *Encelia farinosa*, and *Sphaeralcea ambigua*) and palo verde trees (*Cercidium floridum*). The substrate is a mix of sand, rock, and gravel, and numerous small washes run through the site.

Trapping efforts at Deep Canyon since 1996 have documented 5 heteromyid and 2 murid rodent species in the study habitat type; only 5 of these were captured on the focal study plots. The sole kangaroo rat species and largest heteromyid species was Merriam's kangaroo rat (*Dipodomys merriami*), which often reached considerable densities at the site. The 2nd largest heteromyid and largest of the 3 pocket mouse species was the long-tailed pocket mouse (*Chaetodipus formosus*), by far the most common rodent in the community. Its somewhat smaller congener, the spiny pocket mouse (*C. spinatus*), was

Downloaded From: https://bioone.org/journals/Journal-of-Mammalogy on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

somewhat uncommon but consistently present in the community. The San Diego pocket mouse (*C. fallax*) is intermediate in size to the 2 other pocket mice species, and although it was rare to absent in this habitat in most years, it reached very high densities at the study site during the 1997–1998 ENSO. The sole murid species was the cactus mouse (*Peromyscus eremicus*), which is similar in size to the spiny pocket mouse and also fairly rare but consistently present in the community. The desert woodrat (*Neotoma lepida*) was moderately common at Deep Canyon, but was never captured on these study plots. Finally, Bailey's pocket mouse (*C. baileyi*) occurred rarely at Deep Canyon (D. Kelt, in litt.), which is at the very edge of the geographic range for this species.

The heteromyid rodents of North American deserts are highly adapted to life in deserts and have been subjected to extensive ecological investigation (Genoways and Brown 1993). They are longer-lived and have lower reproductive rates than other rodents of comparable size, and they reproduce only during certain times of year, regardless of food availability. They are subterranean and drought-tolerant species, and their cheek pouches allow them to transport considerable amounts of seeds while foraging. This seed-caching behavior helps them survive the highly variable productivity and food availability that occurs in their desert environments. Heteromyid rodents are solitary as adults (Brown and Harney 1993). The smaller kangaroo rat species, which includes *D. merriami*, generally do not defend their home ranges sufficiently to be considered territorial, and more often cache seeds in shallow scatter-hoards that they move around frequently (Leaver and Daly 2001; Price et al. 2000). At Deep Canyon, pocket mice are primarily larder hoarders (Leaver and Daly 2001). Pocket mice also are not generally considered territorial; however, they do have nonoverlapping home ranges and a behavioral pattern of avoidance (Maza et al. 1973).

Previous studies at Deep Canyon on the caching and cache-stealing behavior of the heteromyid species have shown that the pocket mice regularly pilfer the caches of the kangaroo rats, but that the kangaroo rats do not pilfer from pocket mice caches (Leaver and Daly 2001; see also Murray et al. 2006). A previous resource addition experiment in a heteromyid rodent community in southeastern Arizona showed that the largest kangaroo rat species increased in density, pocket mice species showed no change in density, and the smaller kangaroo rats species actually declined in density, perhaps from increased competition with larger kangaroo rats (Brown and Munger 1985). These results suggest that the largest kangaroo rat species monopolized supplemental food, with little if any additional resources reaching the pocket mice.

Experimental design.—Small nocturnal mammals were surveyed with Sherman live traps (model XLK; H. B. Sherman Traps, Inc., Tallahassee, Florida) on 7×7 trapping grids with 10-m spacing (about 0.49 ha). We established 6 study plots on the valley floor, adjacent to the rocky slopes of the surrounding hills. Study plots were a minimum of 200 m apart to minimize movement of individuals between plots. We paired control and treatment sites to form 3 blocks of 2 sites each, matched according to similarity in substrate and proximity to the adjacent slopes. To ensure the results were not idiosyncratic to any particular section of the study system, the 3 blocks were selected along a mild gradient of substrate type and proximity to the surrounding hills. The study plots for this experiment were located in the same habitat type as the plots of the long-term study (Kelt 1999), with similar vegetation and substrate, but sufficiently far away from those plots that the resource additions in this experiment would not interfere with the long-term study.

A pretreatment census was conducted in November 1999, after which we initiated food supplementation. Subsequent censuses were performed in late December 1999, and in January–February, March, June–July, and November 2000. Each plot was trapped for 3 consecutive nights during each of the 6 sampling periods. All handling of live animals in this study was performed humanely in accordance with guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998), and approved by the University of California's Animal Care and Use Committee. Traps were set at dusk and checked the next morning before sunrise. Because all traps had to be checked before the sun shone directly on them, we sampled only 2 grids at a time; thus, we sampled each block in succession, and each census lasted $3 \times 3 = 9$ days. Traps were baited with millet seed (*Panicum miliaceum*), which we microwaved to prevent germination. Animals were individually marked with numbered metal ear tags (*Dipodomys* and *Peromyscus*) or unique toe clips (*Chaetodipus*), and species, sex, age, mass, and reproductive status were recorded. Trap success varied from low to moderate, with an average of 5–55% of traps being occupied on any given night during a census. Because these species exhibit high trappability (Kelt 1999), we used the total number of individuals captured per census as a metric of population density.

As noted above, our study was conducted during 2 years of relatively low precipitation following the 1997–1998 ENSO event. Supplemental food was provided after trapping sessions in November 1999, December, January, and March, and once again in early April 2000. Thus, 5 pulses of resources were provided during the winter and spring season, coinciding roughly with the winter ''rainy'' season at Deep Canyon. All food additions occurred at least 3 weeks before a given census, and all supplemental food was removed from feeders by rodents in 2 or 3 nights (M. C. Orland, in litt.). The length of time between consumption of supplemental food and trapping sessions makes it likely that censuses reflected resident individuals rather than nonresident visitors to the feeders, and that supplemental food was consumed by resident individuals.

Supplemental food consisted of 9 kg of seed per plot, corresponding to about 90 kg ha^{-1} $year^{-1}$ over the course of the experiment and approximating the seed available to the rodent community during an especially high-rainfall year. No seed productivity data exist for Deep Canyon, but seed production at a southern California Mojave Desert site averaged about 949 kg ha^{-1} $year^{-1}$ (Price and Joyner 1997); mean annual rainfall at that site is about 50% greater than at Deep Canyon. Considering that we excluded nonrodent consumers from our supplemental food (see below), our resource addition

Downloaded From: https://bioone.org/journals/Journal-of-Mammalogy on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

rate likely is an appropriate, and probably conservative, approximation of the resource pulse available to rodents at this site during a high rainfall year such as the 1997–1998 ENSO. Our seed addition rate of 90 kg ha^{-1} $year^{-1}$ also is similar to that of another food-addition experiment in a heteromyid community, which had a supplementation rate of 96 kg ha^{-1} $year^{-1}$ at a Chihuahuan Desert site with an average annual precipitation of 442 mm (Brown and Munger 1985).

Seed was dispensed in 16 feeders at each of the 3 treatment plots, arranged at approximately 15-m intervals. Feeders consisted of L-shaped, 2-inch (about 5-cm)-diameter polyvinyl chloride pipe with fittings that constrained the entrance to 0.75 inches (about 19 mm) in diameter (Meserve et al. 2001), thereby excluding birds and larger rodents (such as kangaroo rats and woodrats). Birds were further hindered by the L-shaped design, and ants were excluded by coating the openings of the feeders with Fluon (AGC Chemicals Americas, Inc., Bayonne, New Jersey). We chose to exclude kangaroo rats from the feeders to ensure the added food would go to the smaller species in the community, because previous studies indicated that the largest kangaroo rat species would likely monopolize any added resources if given the opportunity (Brown and Munger 1985). Because these smaller species are similar in size, they are more likely to partition the added food, so our experimental design increased the likelihood of eliciting an increase in diversity.

Statistical methods.—The design of the experiment allowed us to perform 2 separate statistical tests, which are compared to corroborate the results and give additional insight. The 1st test simply compares plots at the end of the experiment in November 2000 against the same plots just before the experiment began in November 1999 to ascertain the cumulative effects of resource supplementation. We used analysis of variance (ANOVA) to compare abundance, biomass, and the Berger–Parker diversity index (described below) in control and treatment plots at the 1st and last sampling dates. Because the final sampling occurred at exactly the same time of year as the initial sampling, this test inherently controls for both date and plot effects.

For the 2nd statistical test, we applied repeated-measures analysis of variance (rmANOVA) to evaluate the impacts of the food additions on abundance, biomass, and diversity by evaluating the following variables on a per hectare basis (recall that actual grid size was about 0.49 ha): total animals, total adults, total juveniles, total biomass, mean mass of adult *C. formosus*, species diversity (Berger–Parker index), and proportion of the dominant species *C. formosus*. We evaluated mean adult mass for only *C. formosus* because it was the only species that consistently occurred on all plots at all dates. Analyses were conducted on the 2nd through 6th censuses, because the 1st was a baseline measured before food supplementation, and therefore lacked treated plots. However, the 1st data point was analyzed to confirm that there were no detectable differences between plots at the beginning of the experiment.

Diversity indices generally fall into 2 categories—those that emphasize species richness, and those that emphasize species evenness or dominance (Magurran 1988). Given the response of this community to ENSO, where only 1 new species came into the system and there was a dramatic proportional increase in rare species, we selected an evenness metric, the Berger–Parker index (Magurran 1988). We use the standard convention of displaying the Berger–Parker index as $1 - d$ because this is intuitively clearer because d actually increases with decreasing diversity.

We assessed normality for all variables using a 1-sample Kolmogorov–Smirnov test in SYSTAT (SPSS Inc. 1998). The only significantly nonnormal metric was the number of juveniles, which was normalized with a log transformation. We evaluated response variables using a 3-factor ANOVA truncated to only 2-way interactions, for the following factors: block, date, treatment, block × date, date × treatment, and block × treatment. Because there were slight differences in the substrates of our 3 different blocks, to be conservative we did not consider our blocks to constitute ecologically defensible replicates, and we thereby treated the block × treatment interaction as a fixed effect (see Newman et al. 1997). This effectively structures this as a case study in which we are able to quantify ecological responses within our study blocks, but unable to extrapolate these to the regional desert. Most variables were analyzed with Proc Mixed in SAS version 9.1.3 (SAS Institute 2002–2003, Cary, North Carolina); however, for 1 variable (Total Adults) the model did not converge, so we analyzed this using Proc GLM. For those variables that did not show a significant response to food addition, a power analysis was run using the University of Iowa Javascript power calculator (www.stat.uiowa.edu/~rlenth/Power/index.html). Because these rodents reproduce only during the late spring and early summer regardless of food availability, a date × treatment interaction was expected for number of juveniles. We ran a post hoc multiple pairwise comparison with a Tukey adjustment on the number of juveniles so that a difference at any single sampling time would be detectable.

Results

We detected no pretreatment differences in rodent abundance, biomass, or diversity (Figs. 2–4). Total rodent abundance did not differ between November 1999 and November 2000 in the control plots or the treatment plots, although there was a very strong trend toward greater rodent densities in the treatment plots ($F = 17.815$, $d.f. = 1, 2$, $P = 0.052$). Because all of the heteromyid young-of-the-year would have already grown to maturity by November, this comparison of total rodent abundance is essentially a comparison of adult rodent abundance. Total rodent biomass did not differ between November 1999 and November 2000 in the control plots, but was greater in November 2000 for treatment plots ($F = 65.037$, $d.f. = 1, 2$, $P < 0.016$). The Berger–Parker index did not differ between November 1999 and November 2000 in the control plots, but it was lower in November 2000 for the treatment plots ($F = 48.216$, $d.f. = 1, 2$, $P < 0.021$).

Repeated-measures ANOVA indicated that rodent populations were larger in treatment plots ($F = 12.98$, $d.f. = 1, 10$,

Downloaded From: https://bioone.org/journals/Journal-of-Mammalogy on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

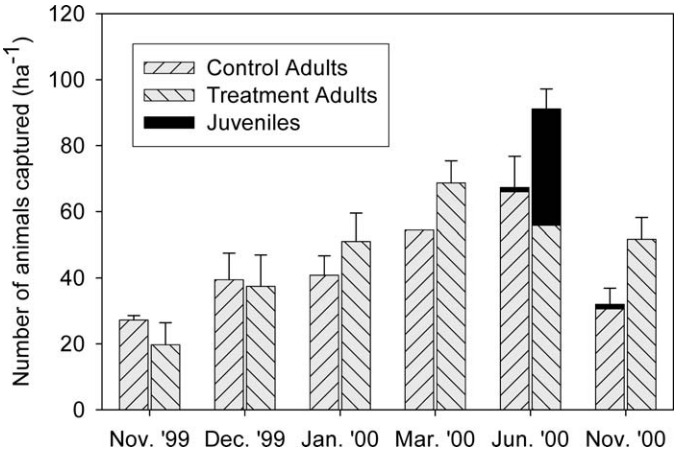


FIG. 2.—Total rodent abundance for control and treatment plots at all sampling dates. Control data are to the left and treatment data to the right in the paired bars at each date. The total number of individuals is significantly higher in supplemented plots, but the total number of adults is not significantly different, suggesting that the home ranges of the adult rodents are invariant to resource abundance. The much greater number of juveniles in the enriched plots indicates that reproduction is highly food limited. Note that data are displayed as animals/ha for comparative purposes, even though the plots were slightly less than 0.5 ha.

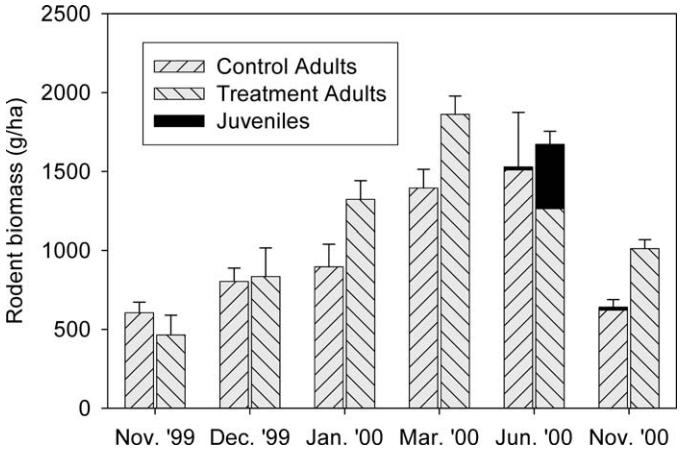


FIG. 3.—Biomass for control and treatment plots at all sampling dates. Control data are to the left and treatment data to the right in the paired bars at each date. Total rodent biomass is greater in the treatment plots, as expected in a food-addition experiment.

$P = 0.0048$), with a mean increase of 13 animals/ha (from 47 to 60 animals/ha; Fig. 2). However, the difference in the density of adults (4 animals/ha), was not significant ($F = 2.29$, $d.f. = 1, 10$, $P = 0.1613$). A power analysis showed that this experiment could detect a difference of 4 animals/ha with a power of 0.13, and a difference of 13 animals/ha with a power of 0.8. The number of juveniles also was significantly greater in treatment plots (35 individuals/ha versus 1 individual/ha; $F = 74.20$, $d.f. = 1, 20$, $P < 0.0001$); all juveniles captured in treatment plots were *C. formosus*. The response of biomass mirrored that of abundance (Fig. 2). Total rodent biomass was 27% higher in the treatment plots (1,050 versus 1,340 g/ha; $F = 7.27$, $d.f. = 1, 10$, $P = 0.0224$), but the total biomass of adult rodents was not significantly greater in the treatment plots ($F = 2.94$, $d.f. = 1, 10$, $P = 0.1170$). Additionally, mean mass of adult *C. formosus* was 15% larger in the enriched plots (20.8 g versus 18.2 g; $F = 32.86$, $d.f. = 1, 10$, $P = 0.0002$).

Of the 5 species previously captured at this site, only 4 were encountered during this experiment (Fig. 4). The San Diego pocket mouse (*C. fallax*) was not captured on any of the experimental plots, nor at other monitoring sites in the valley, for the duration of this experiment (Fig. 1). The Berger–Parker diversity index ($1 - d$) was lower in treatment than control sites (0.34 versus 0.22; $F = 27.02$, $d.f. = 1, 10$, $P = 0.0004$), indicating that supplemental food reduced community diversity. The proportional abundance of *C. formosus* was greater in the treatment plots ($F = 20.49$, $d.f. = 1, 10$, $P = 0.0011$), indicating that this species became more dominant with the resource supplementation. The Berger–Parker diversity index was the only variable that showed a significant block × treatment interaction ($F = 3.27$, $d.f. = 4, 18$, $P = 0.0352$). An interaction plot for this variable (Fig. 5) shows that although 2 of the blocks declined noticeably with the resource additions, 1 remained essentially unchanged.

DISCUSSION

We applied 2 statistical tests to assess the response of a desert heteromyid assemblage to food supplementation over the course of 1 year. Both analyses are in general agreement, and indicate that total rodent abundance and total rodent biomass increased, and species diversity decreased, in response to supplemental food.

Abundance.—Although both density of juveniles and total density increased on treatment plots, no change was observed in density of adults. The 35-fold difference in densities of juveniles in June 2000 suggests that reproduction in this com-

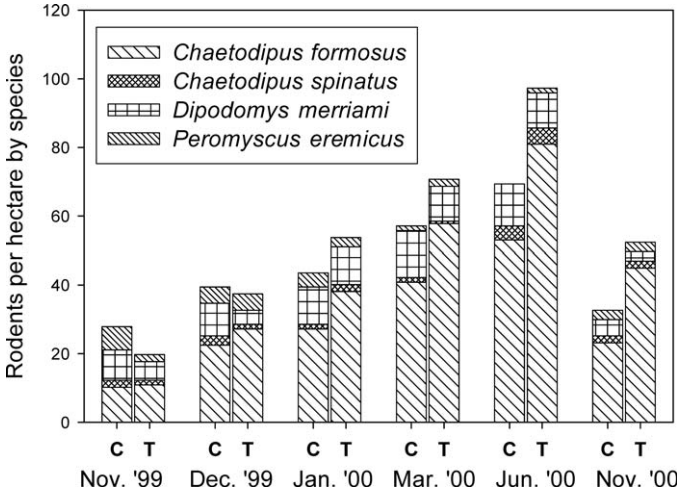


FIG. 4.—Species composition for control and treatment plots at all sampling dates. Control data are to the left and treatment data to the right in the paired bars at each date. *Chaetodipus formosus* appears to have increased disproportionately relative to the other species.

Downloaded From: https://bioone.org/journals/Journal-of-Mammalogy on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

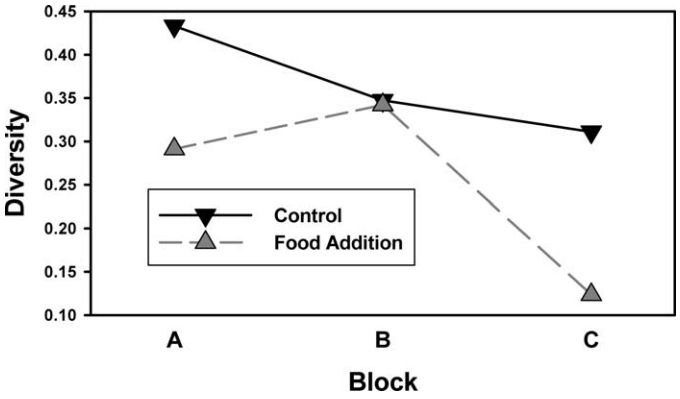


FIG. 5.—Interaction plot for species diversity. Although 2 of the blocks (A, C) showed clear declines in diversity with resource supplementation, the 3rd block (B) did not change. Block B had a large desert wash running through it, and this greater habitat heterogeneity may have prevented *Chaetodipus formosus* from monopolizing the additional resources.

munity was limited by food, as is typical in desert heteromyids (Brown and Harney 1993). All of the juveniles captured in the treatment plots were *C. formosus*, suggesting that only this species was able to convert the pulsed resources to reproductive energy. The low reproduction in the control plots likely reflected limited productivity there, because of the very low rainfall during the study. In contrast to this dramatic increase in densities of juveniles, densities of adults did not change with food supplementation. The observed difference of 2 adult animals per plot seems unlikely to be biologically meaningful, although our experiment lacked statistical power to reliably detect a difference this small.

Our comparison of community metrics before and after resource addition (e.g., November 1999 versus 2000) showed a strong trend toward an increase in total rodent density, although this trend was not quite significant ($P = 0.052$). Because there were very few juvenile animals present at either November sampling, this implies an increase in adult rodents. Although this trend would appear to contradict the results of the rmANOVA, the discrepancy of these 2 results reflects their differing timescales and the influence of seasonal factors. Densities of rodents were highest in June 2000, and at this point the density of adult rodents was lower in the treatments as opposed the controls (Fig. 2). In contrast, by November 2000 the total number of adult rodents was greater in treatment than control plots, but the total number of animals was much lower than in June. This indicates that the supplemental seed was allowing animals on treatment plots to maintain higher densities than on control plots, fully 8 months after the final seed addition. Thus, although food supplementation did not allow for elevated rodent numbers directly, it may have done so indirectly, through differential attrition in summer and fall, reflecting the use of stored seed.

Diversity.—The overall impact of food addition on community composition was to decrease species diversity by allowing increased dominance of the largest pocket mouse and most common species, *C. formosus*. The significant increase in the proportion of *C. formosus* appeared to be due to the ability of this species to better sequester and utilize supplemental resources for reproduction (Fig. 4). The decline in diversity that accompanied the increased dominance was reflected in the lower Berger–Parker ($1 - d$) index in the supplemented plots. The fact that this metric showed a significant block $\times$ treatment interaction (Fig. 5) suggests that species diversity was highly dependent upon microhabitat, consistent with our understanding of the importance of microhabitat to the distribution of heteromyid rodents (Reichman and Price 1993). Although all study plots had desert washes running through them, the block that did not show a change in species diversity with the treatment had a larger wash running through it, with a greater variety of plant species (M. C. Orland, in litt.). This greater heterogeneity could have allowed less-dominant species such as *P. eremicus* and *C. spinatus* to maintain their relative abundance in the community. In contrast to species diversity, abundance and biomass did not exhibit significant block $\times$ treatment effects, which would be consistent with these variables being more dependent upon total energy in the system rather than spatial habitat structure.

Comparison to ENSO.—The decline in species diversity on supplemented plots contrasts with the increase in diversity documented in this assemblage during the 1997–1998 ENSO. This indicates that this small-scale manipulative resource addition experiment did not simulate the same mechanisms as a large-scale, climate-induced productivity pulse. Thus, at least in this system, a manipulative experiment provides limited insight into how climatic variability influences assemblage structure. However, the decline in diversity that we documented is entirely consistent with resource addition experiments elsewhere (Rosenzweig and Abramsky 1993). Various hypotheses have been offered to explain declines in species diversity in augmentation experiments. One of the best-supported hypotheses proposes that resource addition experiments cause diversity to decline because they inadvertently decrease the spatial heterogeneity of resources at the local scale. The homogenization will tend to favor a single species, thereby reducing the opportunity for niche partitioning that was available in a more spatially heterogeneous environment. Our experiment altered the spatial distribution of seeds at a fine scale, which appears to have favored *C. formosus*. Species coexistence in heteromyid communities may be mediated by spatial structure at relatively fine scales and differential seed caching strategies (Price and Waser 1985; Price et al. 2000). Simulation models of a heteromyid rodent assemblage showed that under naturally occurring seed distributions and densities there were multiple optima for utilizing seed patches of different densities; when the distribution or density of seeds differed from the natural distributions, however, all species converged on a single optimum (Reichman and Roberts 1994). This may imply that nearly any supplementation experiment to a heteromyid rodent assemblage would lead to a decline in diversity because the spatiotemporal distribution of seeds would encourage the monopolization of those resources by a single species.

Downloaded From: https://bioone.org/journals/Journal-of-Mammalogy on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

The use of feeders that excluded kangaroo rats, ants, and birds was another difference between how our experiment and the ESNO event distributed the seed pulse to the community. However, there is no a priori reason to believe that this difference would necessarily cause a decline in small mammal diversity. In fact, we excluded kangaroo rats from the feeders to increase that likelihood that the resource additions would be partitioned among the pocket mouse species rather than merely monopolized by the larger kangaroo rats.

Home-range size effects.—The lack of change in the density of adult rodents through the supplementation period suggests that home-range sizes remained essentially constant as resources were increased. Rather than more individuals moving in to take advantage of the resource pulses, the dominant individuals apparently defended their superior habitat and monopolized the added resources. This assumes that the area sampled by the trapping grid was not greatly affected by the resource pulse. Given that trapping sessions occurred $\geq$3 weeks after the allocation of supplemental resources, this likely is a valid assumption. Furthermore, if resource additions did affect the area sampled by the grid, they likely would increase that area, thereby increasing the number of rodents captured per plot. The lack of change in the density of adult rodents suggests that the area sampled by the trapping grids was not greatly influenced by these treatments.

The lack of response in density of adult rodents is contrary to most theoretical predictions and to most other resource addition experiments, which generally show that vertebrates will decrease the size of their home range, increase the degree of overlap with other individuals when resources become more abundant, or both (Boutin 1990). However, our result is consistent with predictions that animals in harsh or highly variable environments will choose not to reduce their home-range size and not to increase overlap with other individuals when resources become more abundant (Levins 1968; Lima 1984; MacLean and Seastedt 1979). Under such conditions an animal may choose to maintain a large home range as a precaution against unpredictable lean times to come. In our community, it is not surprising that *C. formosus*, the largest pocket mouse species at this site, was best able to monopolize resources; it was the only species to increase in proportional abundance and to reproduce in treatment plots.

Our results are consistent with previous research on home-range dynamics of *C. formosus*; spatial distributions among individuals of this species generally are determined by behavioral interactions with other individuals rather than by resource availability (Maza et al. 1973). This same study suggested that fluctuations in the population dynamics of *C. formosus*, and likely other heteromyid species as well, in response to variation in productivity are dampened by behavioral interactions between individual rodents. These insights and our results are consistent with the results of individual-based models (Kendall and Fox 2002; Łomnicki 1999; Uchmanski 1999). At an individual level, maintaining a constant home-range size would be adaptive for species in a harsh and unpredictable environment because energy not allocated to the occupation of a larger home range could be allocated to other needs, potentially increasing survival in the longer term. These models indicate that such behavior would result in less-variable, more-persistent population dynamics in the face of environmental fluctuations.

Similarly, a more territorial species might be less likely to alter its home-range size or to allow for increased overlap in response to a resource pulse. The small kangaroo rat and pocket mouse species at our site are not generally considered territorial because they have not been observed actively defending home ranges, although they actively avoid one another and tend to have much less home-range overlap than expected if space use was random (Maza et al. 1973). The results of our experiment are consistent with those expected for a territorial species, and may suggest that the smaller heteromyids are more territorial than is generally acknowledged. Given the importance of seed caching and of protecting seed caches, it would not be surprising for all the members of this family to be territorial to some degree.

Acknowledgments

We thank S. Lawler, M. Watnick, and N. Willits for their helpful comments and advice during the analysis and writing of this study. We also thank the editor and 2 anonymous reviewers for their thorough comments, which improved the quality of the manuscript. We gratefully acknowledge the assistance of A. Muth, M. Fischer, and D. Herbert of the Boyd Deep Canyon Desert Research Center. This study was funded by a National Science Foundation Graduate Research Fellowship, a University of California, Davis, Jastro-Shields grant, a Sigma Xi grant-in-aid of research, and additional support from University of California, Davis.

Literature Cited

Animal Care and Use Committee. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Canadian Journal of Zoology 68:203–220.

Brown, J. H. 1973. Geographical ecology of desert rodents. Pp. 315–341 in Ecology and evolution of communities (M. L. Cody and J. M. Diamond, eds.). Belknap Press, Cambridge, Massachusetts.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago, Illinois.

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 J. C. Munger. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. Ecology 66:1545–1563.

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.

Genoways, H. H., and J. H. Brown (eds.). 1993. Biology of the Heteromyidae. Special Publication 10, The American Society of Mammalogists.

Holmgren, M., et al. 2006a. A synthesis of ENSO effects on drylands in Australia, North America and South America. Advances in Geosciences 6:69–72.

Downloaded From: https://bioone.org/journals/Journal-of-Mammalogy on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

HOLMGREN, M., ET AL. 2006b. Extreme climatic events shape arid and semiarid ecosystems. Frontiers in Ecology and the Environment 4:87–95.

KELT, D. A. 1999. Assemblage structure and quantitative habitat relations of small mammals along an ecological gradient in the Colorado Desert of southern California. Ecography 22:659–673.

KENDALL, B. E., AND G. A. FOX. 2002. Variation among individuals and reduced demographic stochasticity. Conservation Biology 16: 109–116.

LEAVER, L. A., AND M. DALY. 2001. Food caching and differential cache pilferage: a field study of coexistence and sympatric kangaroo rats and pocket mice. Oecologia 128:577–584.

LEHOUEROU, H. N., R. L. BINGHAM, AND W. SKERBEK. 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. Journal of Arid Environments 15:1–8.

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.

LEVINS, R. 1968. Evolution in changing environments: some theoretical predictions. Princeton University Press, Princeton, New Jersey.

LIMA, S. L. 1984. Territoriality in variable environments: a simple model. American Naturalist 124:641–655.

ŁOMNICKI, A. 1999. Individual-based models and the individual-based approach to population ecology. Ecological Modelling 115:191–198.

MACLEAN, S. F., AND T. R. SEASTEDT. 1979. Avian territory: sufficient resources or interference competition. American Naturalist 114: 308–312.

MAGURRAN, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey.

MAZA, B. G., N. R. FRENCH, AND A. P. ASCHWANDEN. 1973. Home range dynamics in a population of heteromyid rodents. Journal of Mammalogy 54:405–425.

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., W. B. MILSTEAD, AND J. R. GUTIÉRREZ. 2001. Results of a food addition experiment in a north-central Chile small mammal assemblage: evidence for the role of ''bottom-up'' factors. Oikos 94:548–556.

MURRAY, A. L., A. M. BARBER, S. H. JENKINS, AND W. S. LONGLAND. 2006. Competitive environment affects food hoarding behavior of Merriam's kangaroo rats (*Dipodomys merriami*). Journal of Mammalogy 87:571–578.

NEWMAN, J. A., J. BERGELSON, AND A. GRAFEN. 1997. Blocking factors and hypothesis testing in ecology: is your statistics text wrong? Ecology 78:1312–1320.

OEHLER, M. W., SR., R. T. BOWYER, AND V. C. BLEICH. 2003. Home ranges of female mountain sheep, *Ovis canadensis nelsoni*: effects of precipitation in a desert ecosystem. Mammalia 68:385–401.

OWEN, J. G. 1988. On productivity as a predictor of rodent and carnivore diversity. Ecology 69:1161–1165.

PRICE, M. V., AND J. W. JOYNER. 1997. What resources are available to desert granivores: seed rain or soil seed bank? Ecology 78:764–773.

PRICE, M. V., AND N. M. WASER. 1985. Microhabitat use by heteromyid rodents: effects of artificial seed patches. Ecology 66:211–219.

PRICE, M. V., N. M. WASER, AND S. MCDONALD. 2000. Seed caching by heteromyid rodents from two communities: implications for coexistence. Journal of Mammalogy 81:97–106.

REED, A. W., G. A. KAUFMAN, AND D. W. KAUFMAN. 2006. Species richness–productivity relationship for small mammals along a desert–grassland continuum: Differential responses of functional groups. Journal of Mammalogy 87:777–783.

REICHMAN, O. J., AND M. V. PRICE. 1993. Ecological aspects of heteromyid foraging. Pp. 539–574 in Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publication 10, The American Society of Mammalogists.

REICHMAN, O. J., AND E. ROBERTS. 1994. Computer simulation analysis of foraging by heteromyid rodents in relation to seed distributions: implications for coexistence. Australian Journal of Zoology 42: 467–477.

RELYEA, R. A., R. K. LAWRENCE, AND S. DEMARAIS. 2000. Home range of desert mule deer: testing the body-size and habitat-productivity hypotheses. Journal of Wildlife Management 64:146–153.

ROSENZWEIG, M. L., AND Z. ABRAMSKY. 1993. How are diversity and productivity related? Pp. 52–65 in Species diversity in ecological communities (R. E. Ricklefs and D. Schluter, eds.). University of Chicago Press, Chicago, Illinois.

SPSS INC. 1998. SYSTAT 8.0. SPSS Inc., Chicago, Illinois.

TILMAN, D. 1982. Resource competition and community structure. Monographs in Population Biology 17. Princeton University Press, Princeton, New Jersey.

UCHMANSKI, J. 1999. What promotes persistence of a single population: an individual-based model. Ecological Modelling 115:227–241.

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.

VLASMAN, K. L., AND J. M. FRYXELL. 2002. Seasonal changes in territory use by red squirrels, *Tamiasciurus hudsonicus*, and responses to food augmentation. Canadian Journal of Zoology 80:1957–1965.

WHITFORD, W. G. 2002. Ecology of desert systems. Academic Press, San Diego, California.

ZABRISKIE, J. G. 1979. Plants of Deep Canyon. Philip L. Boyd Deep Canyon Desert Research Center, University of California, Riverside.

Submitted 28 January 2007. Accepted 28 November 2007.

Associate Editor was Gerardo Ceballos.

Downloaded From: https://bioone.org/journals/Journal-of-Mammalogy on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use