

Results of a food addition experiment in a north-central Chile small mammal assemblage: evidence for the role of “bottom-up” factors

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Since 1989, effects of biotic interactions including predation and herbivory have been examined in a replicated experimental study in a north-central Chilean semiarid thorn scrub community. Strong responses of small mammals and plants to El Niño Southern Oscillations (ENSO) have also been documented suggesting that “bottom-up” factors related to high rainfall are important. To simulate increased primary productivity effects on small mammals, ad lib rabbit pellet additions were initiated in mid-1997 on unfenced grids near the experimental complex. Following the 1997 El Niño event with three times normal precipitation, numbers of small mammals during pre-addition months and the first treatment year were similar on control and food addition grids. During the second year (1998–1999), a period of severe drought, food additions had significant positive effects on numbers of two predominantly herbivorous “core” (resident) species, *Octodon degus* and *Phyllotis darwini*, and an omnivorous “quasi-core” (resident but highly fluctuating) species, *Akodon olivaceus*; however, all three species declined towards the end of the second treatment year. Two “opportunistic” (temporarily resident) species, *Abrothrix longipilis* (an insectivore) and *Oligoryzomys longicaudatus* (a granivore), showed no responses to food additions. An insectivorous marsupial, *Thylamys elegans* (also a “core species”), had significantly lower numbers on food addition grids. Changes in body weight distributions and proportions of reproductive individuals particularly in *O. degus* indicate in situ responses. Whereas no differences in residency, numbers of stations visited, and trappability were observed, energy compensation ratios greater than one suggest significant immigration in the second year. Thus, food additions elicited strong responses by herbivorous/omnivorous “core” and “quasi-core species” whereas they had no effects on “opportunistic species”. These results reinforce the view that “bottom-up” factors influencing food availability exert prevailing control on numerically important small mammal species by temporarily increasing carrying capacity, and that “top-down” factors (i.e., biotic interactions) become important when small mammal numbers are at or near their carrying capacity. Spatial dynamics may be important in explaining declines of species populations exhibiting initially positive responses to food additions.

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The role of “bottom-up” vs “top-down” factors in community ecology has been hotly debated. Various hypotheses which predict largely “top-down” control (e.g., the “World is green” hypothesis or “HSS” for

Hairston et al. 1960, Slobodkin et al. 1967) have been amended to account for differing levels of productivity (e.g., the “Exploitation ecosystem hypothesis” or “EEH”; Oksanen et al. 1981, Oksanen 1992, Oksanen

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and Oksanen 2000). On the other hand, purely “bottom-up” hypotheses (e.g., White 1978, Hunter and Price 1992) predict that all trophic levels are essentially limited by available resources (i.e., “donor-controlled”; Polis and Strong 1996), and that “top-down” biotic interactions (i.e., predation, herbivory) are relatively unimportant. Even if biotic interactions can be shown to have “primacy” (sensu Power 1992) in controlling lower trophic levels, their role must be viewed against a background of constantly changing abiotic conditions (e.g., Wiens 1977, 1986, 1989, Wiens et al. 1986). Yet, environmental fluctuations and harshness per se do not preclude the importance of biotic interactions (Chesson and Huntley 1997). Clearly, if consumers can depress their resources or prey, thus exerting controlling influences on their food, some degree of “top-down control” is operating; if on the other hand, resource availability is more strongly tied to abiotic factors independent of consumer effects, “bottom-up control” may be said to be operating (Power 1992). The resolution of these dichotomous arguments may lie in a pluralistic view that recognizes that both “top-down” and “bottom-up” control can operate at different times (e.g., Hunter and Price 1992, Power 1992).

Arid systems offer unusual opportunities to investigate the role of “top-down” vs “bottom-up” control because of high variability of rainfall both within and between years. In the Western Hemisphere, arid regions often have high rainfall associated with El Niño Southern Oscillation (ENSO) events, leading to shifting conditions in which “top-down” (primarily biotic interactions) vs “bottom-up” (primarily abiotic factors) control may have “primacy”. However, the small temporal and spatial scale of most field experiments (Sih et al. 1985, Kareiva and Anderson 1988, Tilman 1989) results in difficulty distinguishing the relative importance of these elements in long-term community organization. Large-scale studies (particularly long-term ones) are often necessary to demonstrate the subtle interplay of biotic and abiotic factors. They also offer opportunities for integrating information from different organizational levels (Levin 1992) and the study of slow phenomena, rare events, subtle plus complex processes (sensu Franklin 1989, Pickett 1991), or hidden ones in the “invisible present” (Magnuson et al. 1991).

Since early 1989, we have conducted a large-scale manipulation in a semiarid locality in north-central Chile with primary focus on the importance of biotic interactions, specifically vertebrate predation, interspecific competition, and herbivory, on the small mammal assemblage and plants using a “press” approach (sensu Bender et al. 1984). Our results (e.g., Meserve et al. 1993a, b, 1996, 1999, Gutiérrez et al. 1997) established the importance of biotic interactions on several small mammal and plant species. However, populations of small mammals and plants in the Chilean semiarid region also show strong fluctuations, particularly in

response to high rainfall during El Niño events (e.g., Fulk 1975, Pearson 1975, Péfaur et al. 1979, Fuentes and Campusano 1985, Meserve and Le Boulengé 1987, Dillon and Rundel 1990, Jiménez et al. 1992, Meserve et al. 1995, Gutiérrez et al. 1997). In a sense, El Niño (and ensuing La Niña) events are natural “pulse” experiments that alter the role of biotic vs abiotic factors. Thus, such factors can have varying importance depending on background environmental conditions (Meserve et al. 1999).

A crucial test of whether “bottom-up” factors exert strong effects on small mammal populations is provided by food addition experiments, especially where they simulate the consequences of naturally occurring environmental phenomena such as El Niño events. Although food itself is a biotic factor, its availability may be triggered by abiotic events such as precipitation. In north-central Chile, El Niño events result in dramatic increases in primary productivity and plant cover following episodes of unusually high precipitation (Gutiérrez et al. 1997). The lack of significant depression of plant cover and biomass by small mammal folivores (Gutiérrez et al. 1997), and evidence for strong effects of nutrients and water on primary productivity (Gutiérrez 1993) suggest that precipitation acts as an ultimate factor, and food as a proximate one in the system. A review of 62 food addition experiments with small mammals (Boutin 1990) reported varying responses including increased reproduction and body weight, decreased home range size, and on average, a two-fold increase in population densities. However, few such studies have been conducted in contrasting periods of environmental conditions with attention to the relevance of food as a proximate “bottom-up” factor. Herein we report the results of such an experiment conducted over two years in semiarid Chile during and following an El Niño event in 1997.

Our hypotheses are the following. First, during and immediately following the 1997 El Niño event (1997–1998) when background food availability was high due to higher precipitation, there should have been no differences between control and food addition treatments. However, in the ensuing La Niña (drought) event (1998–1999), differences should have become apparent as food levels declined on control grids. Second, species differences in responses should be present; herbivorous to omnivorous small mammals such as *Octodon degus*, *Phyllotis darwini* and *Akodon olivaceus* should show stronger responses to food additions than insectivorous or granivorous species such as *Oligoryzomys longicaudatus*, *Abothrix longipilis* and *Thylamys elegans*. Besides numerical increases, other responses were expected in positively responding species including changes in body size, reproduction, and residency times. Changes in body size and reproductive rates of individuals should be largely a consequence of in situ processes. The extent to which ex situ processes such as

immigration and greater range of spatial utilization accounted for numerical differences should be reflected in differences in residency, numbers of trap stations visited, and perhaps trappability. The latter could also reflect the potential for trap competition when numbers of animals were particularly high. Finally, a measure of the ratio of energy fixed in the form of small mammal tissue to energy added as food (termed the energy compensation ratio) should indicate whether small mammals exhibit proportional (ratios $\cong 1.0$) or nonproportional (ratios $\neq 1.0$) responses to food additions; greater than proportional responses (ratios > 1.0) would most likely be the result of immigration.

Study area and methods

Study site

The study site has been previously described (Meserve et al. 1993a, b, 1995, 1996, 1999). Briefly, it is in Parque Nacional Bosque Fray Jorge, Chile (71°40'W, 30°38'S; IV Region) 100 km S La Serena and 350 km N Santiago and 2.5 km E of the Pacific Ocean. This 10 000-ha World Biosphere Reserve is primarily semi-arid thorn scrub, but also has isolated fog forests on coastal ridges that have been protected from grazing and disturbance since 1941. The flora of the lower elevational scrub zone includes spiny drought-deciduous and evergreen shrubs and understory herbs on a predominantly sandy substrate (Muñoz and Pisano 1947, Gutiérrez et al. 1993a, b). The climate is semi-arid mediterranean with 90% of the precipitation in winter months (May–September); summer months are warm and dry. Mean annual precipitation is 110 ± 31.7 (1 SE) mm (1989–1999), but coastal fog and high humidity produce dew that ameliorates aridity. During the period of this study, an El Niño in 1997 resulted in 330 mm of precipitation followed by 2.2 mm and 58.5 mm in 1998 and 1999, respectively, during the ensuing La Niña (drought) event.

Although 10 species occur in the small mammal assemblage, focal species here include the herbivorous degu (*Octodon degus* (Molina)), the herbivorous-granivorous leaf-eared mouse (*Phyllotis darwini* (Waterhouse)), the omnivorous olivaceous field mouse (*Akodon olivaceus* (Waterhouse)), the granivorous long-tailed rice rat (*Oligoryzomys* [*Oryzomys*] *longicaudatus* (Bennett)), and the insectivorous long-haired field mouse (*Abrothrix* [*Akodon*] *longipilis* (Waterhouse) and elegant mouse opossum (*Thylamys* [*Marmosa*] *elegans* (Waterhouse)) (dietary descriptions from Meserve 1981a). These species have been previously characterized as “core species” (*O. degus*, *P. darwini*, *T. elegans*) due to their persistence in the thorn scrub, “quasi-core species” (*A. olivaceus*) due to strong oscillations during and following El Niño events with persistence only at

low densities in intervening dry years, and “opportunistic species” (*O. longicaudatus*, *A. longipilis*) due to their disappearance from the thorn scrub in dry years (Meserve et al. 1999).

Methods

In early 1989, we established 16–75 m \times 75 m (0.56 ha) grids in the valley (henceforth, “central grid complex”). The design of the original study includes fenced plots which selectively exclude predators, larger herbivorous small mammals (i.e., degus), or both using different fencing heights, presence/absence of overhead netting, and presence/absence of holes in the fencing (see Meserve et al. 1993a, b, 1995, 1996, 1999 for details). For purposes of this study we used four control grids in the complex which have low (1.0 m high) chicken wire fencing buried ca 40 cm into the ground and ca 5 cm diameter holes every 1–2 m at ground level, thus allowing all predators and small mammals access. For food addition treatments, we used four unfenced 0.56-ha grids located N and S of the central grid complex in similar habitat. Although these grids lacked fences unlike controls, we have found no evidence that fences with access holes act as significant barriers to small mammal movements.

From June 1997 on, we live-trapped small mammals for four nights per month on each grid (5 \times 5 stations, 15 m interval, two traps/station) and marked all captured animals with ear tags or leg bands. Standard data were collected on species, weight, sex, reproductive condition, and presence/absence of ectoparasites during handling. Traps were left open continuously during winter months and checked twice daily; during some warmer summer months, they were closed after the morning check, reopened at mid-afternoon, and rechecked at dusk. Monthly trappability was high for the focal species ($> 80\%$), except for *O. degus* ($\bar{X} = 79\%$) and *T. elegans* ($\bar{X} = 69\%$) enabling use of minimum number known alive (MNKA) estimates of abundance.

After a three-month pre-treatment period (June–August 1997), food additions were initiated on the open grids in August 1997 using “L”-shaped PVC containers with a 10.9 cm diameter entry opening at one end located at each trap station on the ground. Each apparatus was 27.8 cm long on the entry end and 21.2 cm long on the shorter (refilling) end. The food was ad lib rabbit pellets replaced monthly with monitoring of amounts consumed. The containers were closed during censuses, refilled, and opened at the end of the trapping session. Feces and field observations indicated that only small mammals consumed food placed inside the containers during the study.

The experiment allowed comparison of responses of small mammals to food additions between controls and

treatments with grids being the replicates (four/treatment). The data were analyzed with one-way repeated measures analysis of variance (rmANOVA, PROC MIXED; Wolfinger and Chang 1995, SAS 1996) using MNKA estimates of species abundance. Mixed model rmANOVA is a newer SAS procedure that allows for specification of the covariance structure unlike traditional rmANOVA (SAS PROC GLM) which assumes equal levels of covariance among all levels (the circularity assumption, Potvin et al. 1990, von Ende 1993). PROC MIXED allows the testing of a wide range of covariance structures and selection of the one best approximating the data, and hence, use of uncorrected *F*-tests. Here, compound symmetry, auto-regressive, unstructured and Huyn-Feldt covariance structures were compared for each model and the one that maximized Schwarz's Bayesian criteria selected. A further advantage of PROC MIXED is that it calculates least squares means adjusted for covariance structure for all main effects and interactions. As a result, significant interaction terms can be decomposed and means compared by a posteriori *F*-tests to identify points of heterogeneity in time. We tested residuals for normality (SAS PROC UNIVARIATE and departures for normality were analyzed graphically to ensure that the ANOVA assumption of homoscedasticity was met (Stevens 1992). Statistical significance was arbitrarily set at $P \leq 0.05$.

To evaluate responses other than in abundance, we conducted a series of contrasts between several population parameters during September–August 1997–1998 and September–August 1998–1999. The parameters included: 1) body weight distributions; 2) proportions of reproductively active individuals (for males: scrotal condition; for females: perforate, pregnant or lactating condition); 3) sex ratios; 4) residency time (number of months in each 12-month period in which individuals were present); 5) number of stations visited/individual/grid for each 12-month period; and 6) trappability for each 12-month period (number of months in which individuals known alive were captured at least once/census for each 12-month period excluding first and last capture dates). The first three contrasts provide direct information on demographic responses to additions; the latter three the extent to which behavior may have been altered by food addition. Preliminary visual inspection of trends resulted in elimination of many comparisons for lack of obvious differences; for specific statistical comparisons, the Kolmogorov-Smirnov test was used for parameter 1) and chi-square tests with Yates' correction for continuity for the remainder. In these analyses, individuals were pooled from all grids in a treatment (control or food addition) to increase sample size. Again, statistical significance was set at $P \leq 0.05$.

Finally, we assessed the relationship between the amount of food provided and corresponding changes in small mammal biomass. Because of large variation in

body size, and hence, metabolic rates, we followed Brown and Munger (1985) in scaling mass measurements to energy consumption rate (ECR; in kJ/day). Due to obvious differences between the two years in which the additions were conducted, we analyzed them separately. The number of unique individuals (*N*) and the mean weight in kg (*M*) for each species were calculated by grid and year and converted to ECR with the following equation: $ECR = N \times 753 M^{0.67}$ (Brown and Munger 1985). Total energy input was estimated as the amount of food pellets (in kg) consumed in each grid per year multiplied by 17 700 kJ/kg (metabolizable energy, F. Bozinovic pers. comm.), and converted to a daily rate (kJ/day) by dividing by 365. It is assumed that adding energy into the system (in the form of food) will lead to a change in biomass and a concomitant alteration in the ECR. Therefore, responses are measured as the difference in mean ECR (ΔECR) between the treatments and the control and expressed as a ratio between the ΔECR and the mean energy input as food in treatment grids. The ratio of the two values is an estimate of the degree of compensation (sensu Brown and Munger 1985). Ratios less than, equal to, or greater than 1.0 indicate less than, equal to or greater than proportional responses by the corresponding small mammal species. Although we recognize that species differing in diets may have different assimilation efficiencies, use of a high conversion figure for concentrated pellet food as the multiplicand in the denominator of the ratio renders our comparisons conservative.

Results

Fig. 1 shows the numerical responses of all six species from June 1997 through August 1999. Before initiation of food additions (September 1997), no differences in *Octodon degus* numbers were present between control and addition grids ($F_{1,6} = 1.13$, $P = 0.328$). The overall difference for the effect of food during the following two years was significant ($F_{1,6} = 20.9$, $P = 0.004$); however, persistent differences did not become apparent until September 1998 (Fig. 1). Numbers of degus reached 18.8 individuals/food addition grid (compared to 9.3/control grid) peaking in November–January 1998–1999 before starting a slow decline. The sharp decline in August 1999, however, was partially due to removal of degus by foxes (*Pseudalopex culpaeus*); 2–8 individuals were taken (no previous removal had been recorded from food addition grids). It is notable that populations on food addition grids exceeded the maximum observed on control grids following the 1997 El Niño; that is, food additions elicited a numerical response that was greater than that produced by the preceding year's above-normal precipitation. *O. degus*

also showed a significant difference in weight distributions with significantly heavier individuals on food addition grids in both 1997–1998 and 1998–1999 ($P < 0.01$ and 0.001 , respectively, Kolmogorov-Smirnov two-tailed test). However, individuals were also significantly heavier on both controls and food addition grids in 1998–1999 (vs 1997–1998) suggesting a post-El Niño effect ($P < 0.001$). Reproductive activity was higher on food addition grids for both males and females in 1998–1999 ($\chi^2 = 5.4$ and 5.7 , $P = 0.02$, respectively), but not 1997–1998. Sex ratios, residency time, number of stations visited, and trappability did not differ during 1997–1998 or 1998–1999 for treatments or years (all $P > 0.05$).

Phyllotis darwini numbers were higher in food addition grids for two out of three months during the pre-treatment period leading to an overall pretreatment effect ($F_{1,6} = 12.9$, $P = 0.012$); however, numbers converged over time in the first year after initiation of food additions (Fig. 1). A significant treatment \times time interaction indicated a change in *P. darwini* responses over time after food additions started ($F_{23,138} = 2.54$, $P = 0.0005$); an a posteriori F -test for monthly differences showed significant differences from December 1998 through August 1999 (all $F_{1,138} \geq 9.13$, $P \leq 0.003$). Overall, food effects were significant ($F_{1,6} = 12.2$, $P = 0.013$). *P. darwini* numbers on food addition grids did

not exceed the levels on controls in response to the 1997 El Niño, but persisted for several months after they had started to decline on control grids. This species also showed a slow decline after March 1999. Although this species is an important prey for many predators (Silva et al. 1995, Jaksic et al. 1997), it did not show a sharp decline in August 1999 when predation due to removal from traps exerted an effect on *O. degus*. *P. darwini* individuals were significantly heavier on food addition grids (vs controls) in both 1997–1998 and 1998–1999 ($P < 0.001$) as well as on food addition grids during 1997–1998 vs 1998–1999 ($P < 0.001$). Remaining population parameters did not differ between control and food addition grids in 1997–1998 or 1998–1999, or between years.

Numbers of *Akodon olivaceus* were nonsignificantly different on control and food addition grids in the pre-treatment period ($F_{1,6} = 0.29$, $P = 0.613$); numbers diverged from October 1998 on (Fig. 1). A significant overall effect existed for the food addition period with higher numbers then ($F_{1,6} = 13.2$, $P = 0.011$). Similar to *O. degus* and *P. darwini*, a decline was present after October 1998. *A. olivaceus* individuals were significantly heavier on food addition grids (vs controls) in both 1997–1998 and 1998–1999 ($P < 0.01$ and 0.001 , respectively), and significantly heavier on food addition grids in 1997–1998 (vs 1998–1999; $P < 0.001$). There was no difference in reproductive activity between treatments or years, but a biased sex ratio towards males existed on all treatments and years with significant differences between controls and food addition grids in 1997–1998 but not 1998–1999 ($\chi^2 = 7.4$, $P < 0.01$). There were no significant differences in remaining parameters by treatment or year.

Similar to *A. olivaceus*, no differences in numbers of *Thylamys elegans* were present in pre-treatment periods before initiation of food additions ($F_{1,6} = 3.02$, $P = 0.133$; Fig. 1). A significant overall effect of food additions was observed ($F_{1,6} = 10.6$, $P = 0.017$) with, however, a continuous pattern of lower *T. elegans* numbers in food addition grids from August 1998 on. Populations of this species actually increased somewhat on control grids whereas they declined to lower levels on food addition grids until August 1999. *T. elegans* individuals were significantly heavier on control vs food addition grids in 1997–1998 ($P < 0.001$) but not 1998–1999, and in 1997–1998 vs 1998–1999 ($P < 0.05$) for control grids only. No other population parameters were significantly different between treatments or years.

Abrothrix longipilis and *Oligoryzomys longicaudatus* showed no differences in numbers during the pre-treatment period ($F_{1,6} = 0.00$, $P = 1.000$ and $F_{1,6} = 0.18$, $P = 0.686$, respectively) nor in the post-treatment between controls and food addition grids overall ($F_{1,6} = 0.87$, $P = 0.388$ and $F_{1,6} = 0.22$, $P = 0.654$, respectively; Fig. 1). Numbers for *A. longipilis* were low but similar by treatment as it increased following the 1997 ENSO

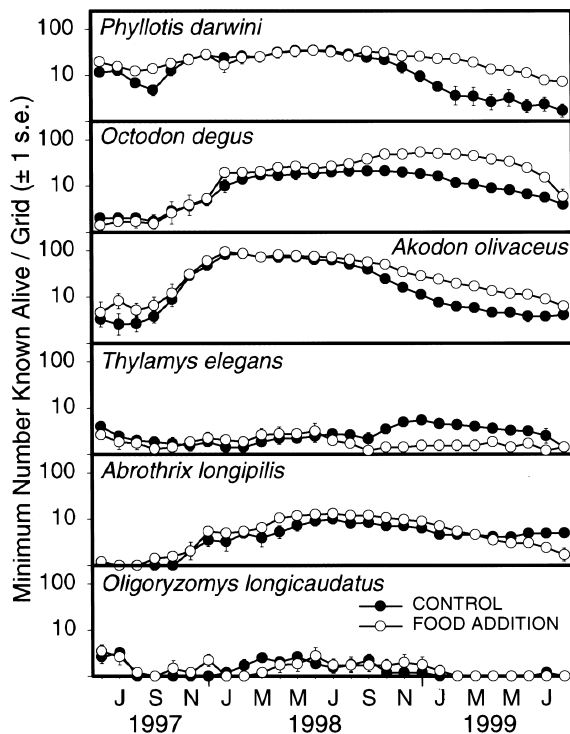


Fig. 1. Population trends of six small mammal species on control and food addition grids during June 1997 through August 1999. June–August 1997 was a pre-addition period.

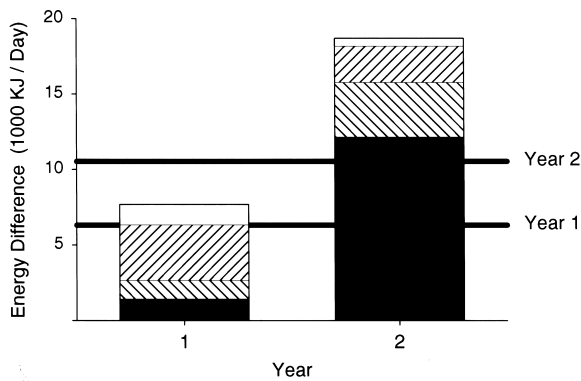


Fig. 2. Cumulative difference in ECR (Δ energy consumption rate; 1000 kJ/day) between treatments and controls by year. Core species shown individually are *O. degus* (solid bar), *P. darwini* (left-hatched bar), and *A. olivaceus* (right-hatched bar); all other (opportunistic) species are included in clear bar. Solid lines indicate mean amount of energy (1000 kJ/day) added to manipulation grids in 1997–1998 (Year 1) and 1998–1999 (Year 2) where the energy compensation ratio = 1.0 for corresponding periods. See text for details of calculations.

and then declined slowly. Although there were no differences in weight distributions between treatments, both control and food addition *A. longipilis* individuals were significantly heavier in 1997–1998 vs 1998–1999 ($P < 0.001$). In 1997–1998, reproductive activity was significantly higher for males in control grids, and sex ratios were significantly less biased towards males than in food addition grids ($P = 0.01$, and $P = 0.03$, respectively). No other population parameters were significantly different for *A. longipilis* by treatment, sex or year. Numbers of *O. longicaudatus* were sporadic and low, typical for this “opportunistic species” in the thorn scrub. No significant differences in population parameters existed by treatment, sex or year for this species.

Compensation ratios for all small mammals combined were greater than one in both years (Fig. 2) indicating that the magnitude of response was greater than expected. During the first year (1998–1999), the cumulative ratio for positively responding “core species” (i.e., *O. degus*, *P. darwini* and *A. olivaceus*) was very close to one suggesting close compensation. During the second year, however, large increases in the biomass of the larger *O. degus* yielded a compensation ratio of 1.16 for this species alone. Cumulatively, *O. degus* + *P. darwini* + *A. olivaceus* had a compensation ratio of 1.68 in the second year (Fig. 2). “Opportunistic species” (i.e., *A. longipilis*, *O. longicaudatus*, etc.) had a combined ratio of 0.21 in the first year, and only 0.05 in the second. In situ processes such as predation, competition, consumption by non-target species, and entropy should lead to reductions in the compensation ratios. Although trends in residency, numbers of traps visited, and trappability were not statistically different for controls and food addition grids, immigration is clearly

implicated as the most reasonable explanation for this outcome.

Discussion

Our results clearly establish the role of food as an important factor influencing the numbers and other demographic parameters of two “core species” (*O. degus* and *P. darwini*) and one “quasi-core species” (*A. olivaceus*). As expected, differences became apparent in the second year of food additions, but not the first following the 1997 El Niño. Two “opportunistic species” (*A. longipilis* and *O. longicaudatus*) were unaffected by food; as insectivorous and granivorous species, respectively, they were not expected to respond strongly to rabbit pellet additions. A sixth insectivorous species (*T. elegans*) was negatively affected by food additions. The latter result is strong inferential evidence for effects of interspecific competition with species responding positively to food additions. Since there are strong dietary differences between *T. elegans* and other species (Meserve 1981a), and it is semiarborescent unlike the more scansorial/terrestrial habits of the three “core/quasi-core species” (Meserve 1981b) that demonstrated positive responses to food additions, interference rather than exploitation competition is implicated. The most likely competitors are *O. degus* and/or *P. darwini* which are both conspicuously larger than *T. elegans*. Negative behavioral interactions perhaps involving territorial defense may also be involved since *Thylamys* is a predatory species that may attack young of other species in the nests.

With the exception of body weight distributions for *O. degus*, *P. darwini*, and *A. olivaceus*, greater reproductive activity for *O. degus* on food addition grids, and some sex ratio differences (*A. olivaceus*, *A. longipilis*), there were few significant positive differences in population parameters in response to food additions. Since there were no differences in residency time, numbers of traps visited, or trappability by positively responding species such as *O. degus* and *P. darwini*, it appears that changes in food conditions influenced *in situ* dynamics. Trap competition did not appear important in explaining differences between control and food addition grids. Heavier weight distributions of *O. degus*, *P. darwini*, and *A. olivaceus* suggest a direct positive effect of food on body size and/or persistence of those individuals in the trappable population.

An alternative interpretation of the decline of small mammals in the second year suggested by an anonymous reviewer is the “pantry effect” in which predators focus in on areas of higher populations, thus depressing local population levels (Ford and Pitelka 1984). We have previously shown that predation effects are greatest during and immediately following El Niño events when small mammal populations typically increase dra-

matically (e.g., Meserve et al. 1996, 1999), and that predators exhibit rapid responses to increased prey abundance, but eventually decrease as overall prey abundance declines (Silva et al. 1995, Jaksic et al. 1997, Salvatori et al. 1999). Although we cannot exclude the possibility of such an effect particularly towards the end of the study, we do note that even typically unutilized prey species such as *A. olivaceus* declined in 1998–1999 along with *O. degus* and *P. darwini* (Fig. 1), and that the expected consequences of prey removal by predators (residency time, number of traps visited, trapability) did not differ between treatments in 1998–1999. Finally, removal of animals from traps was noted only in the last month of the experiment for *O. degus*. Therefore, we view the evidence for a “pantry effect” as weak. Finally, although we used unfenced food addition grids, this avoided potential problems of closed populations that could suffer from overpopulation due to restricted emigration (i.e., the “fence effect” sensu Krebs and Tamarin 1969; but see Ostfeld 1994).

It is significant that continued addition of rabbit pellets was not sufficient to maintain populations of three species that initially responded positively. Although precipitation in 1999 was much higher than in 1998 (58.5 vs 2.2 mm), it was still well below normal; ephemeral plant cover in 1999 was 31.6% for control grids and 28.3% for food addition grids (vs 87.2% and 90.4% for 1997, and 0% and 0% for 1998, respectively). In 1991 and 1992 (both El Niño years with 233 mm and 229 mm, respectively), ephemeral cover peaked at 80.0% in 1991 but declined to 54.0% in 1992 (control grids) suggesting a nutrient depletion effect (Gutiérrez et al. 1997). In contrast, perennial shrub cover has remained virtually constant over more than 50 years of observation in the community (Muñoz and Pisano 1947, Meserve 1981b, Gutiérrez et al. 1997).

We suggest that the decline of all three “core/quasi-core species” towards the end of the second year may indicate the importance of spatial (peripheral) processes. Polis et al. (1997) emphasized the importance of spatial subsidies in food webs including movements by individuals between adjacent habitats. We suggest that observed declines occurred following unsustainably high immigration rates into the food addition grids during times of decreasing food availability in the larger semiarid matrix. The proposed mechanism for this decline is similar to that for “pseudo-sinks” (sensu Watkinson and Sutherland 1995) in which immigration increases local populations to levels that cannot be supported by local resources and results in negative growth rates. During and immediately following the El Niño event in 1997–1998, the changes in carrying capacity produced by food additions mimicked the changes that occurred in the larger thorn scrub community due to predominantly “bottom-up” factors (i.e., precipitation and increased productivity). Hence, trends were similar on treatments and controls in the first year

of food additions when resource levels were high in all thorn scrub areas. Eventually, compensation ratios of much greater than one were documented. However, many more individuals were present on the grids than could be supported by local conditions, especially during and following a very low rainfall year (1998); as a result, differences became accentuated between treatment and controls. In the absence of significant immigration from surrounding habitats, and given a highly seasonal reproductive pattern, grid populations collapsed down to control grid levels towards the end of 1998–1999. Therefore, we believe that these results highlight problems with all field studies that do not address the role of larger spatial processes in local population dynamics.

Other studies have shown less than proportional responses to food additions (i.e., Brown and Munger 1985, Brown et al. 1986, Yunger in press), or proportional effects (Desy and Batzli 1989, Krebs et al. 1995) as well as behavioral responses (Desy et al. 1990). In combination with predator exclusions, effects of food addition have been found to be additive (Desy and Batzli 1989), or multiplicative (Krebs et al. 1995). Since we did not manipulate both predation and food in these experiments, we cannot assess the latter aspect, but predation had small numerical effects on *O. degus* and no effects on the other species and only at the beginning of the study period, suggesting that responses would have been non-multiplicative on the former species, and both non-additive and non-multiplicative on the remaining ones.

Overall, these results reinforce our view that “top-down” factors (i.e., predation) have their strongest effects in years during and immediately following El Niño years (when prey populations are at or near their carrying capacity and of sufficient size to support a stable predator guild); intra/interspecific competition for limited resources may be important at the opposite extreme (i.e., when prey populations are at or near their lowest levels). Recently, Lima and Jaksic (1998a, b, c, Lima et al. 1999) have emphasized the role of density-dependent processes in one of the species here, *P. darwini*. Although they focused on intrinsic regulation, they also recognized that density dependence could include biotic interactions such as predation, and that environmental factors play an important role. Here, we view “bottom-up” factors as prevailing during intervening dry years between El Niño events. The lesser importance of biotic interactions such as predation in dry years is largely due to complex spatial and temporal dynamics of both the most important predators (foxes and owls), and the resident small mammals. As potential prey decline in the larger spatial matrix, predators emigrate or become infradispersed, thus lessening their impact. Time lags in numerical and functional responses by predators result in effects that persist only for a short time after El Niño years (Silva et al. 1995,

Jaksic et al. 1997, Salvatori et al. 1999). As the overall population densities of small mammals decline, opportunities for immigration into artificially augmented food addition grids also decrease. Whereas “bottom-up” factors may be viewed as having overriding control, and their effects can be mimicked by use of food addition experiments, it is important to emphasize that without adequate immigration, local population responses may be eventually dampened. Hence, spatial dynamics of the overall small mammal assemblage has a strong impact on local responses. Only when precipitation becomes sufficient to elicit strong responses by the ephemeral plant community (including seeds) in all habitats and subsequently, the small mammals, would we expect to see a reversal of these declines. Therefore, we predict that in subsequent years with normal or near-normal rainfall with increases in small mammal populations community-wide, there should be a return to strong responses to food additions. Different factors may operate at different times; here predation seems higher when small mammal (prey) populations are high. When resource levels decline, larger scale spatial processes and perhaps, competition may be important for small mammals here.

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