

FORAGING ECOLOGY OF SMALL MAMMALS IN SEMIARID CHILE: THE INTERPLAY OF BIOTIC AND ABIOTIC EFFECTS

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Abstract. We report on the foraging behavior of three small-mammal species over 2½ years using experimental foraging trays. Trays provisioned with oat seed were set out in the field at dawn and dusk, and the amount of seed consumed (with re-provisioning) was determined over three consecutive nights and days. Experiments simultaneously evaluated the role of lunar phase, season, and microhabitat (shrub vs. open); additionally, artificial exclosures (~0.56 ha) were employed to evaluate the influence both of mammalian and avian predators and of a dominant competitor species, the large diurnal degu (*Octodon degus*). Other principal small mammals included Darwin's leaf-eared mouse (*Phyllotis darwini*) and the olive field mouse (*Akodon olivaceus*). Trays were enclosed by hardware-cloth cages with either small or large holes in the side to exclude avian consumers and provide selective access to all small mammals (large holes) or to exclude the largest species (small holes). Small-mammal population sizes varied greatly throughout the study. Principal factors affecting seed consumption rates were population size, followed by season (winter > summer), and microhabitat (shrub > open). The role of the latter factors was relatively minor in 1999 and 2000 but amplified greatly in the final year of study when small-mammal numbers increased five-fold. In contrast to earlier work at this site, predation had minimal direct effects on foraging activities, although significant effects of microhabitat, lunar phase, and season suggest the importance of perceived predator risk. Both *Phyllotis* and *Akodon* foraged more in the absence of degus, and two- and three-way interactions further supported an important role for competition in this system. The combination of large-scale predator/competitor manipulations with fine-scale foraging experiments and long-term replication illustrates the importance of utilizing such approaches to gain insights to behavior and foraging strategies in variable environments.

Key words: *Akodon olivaceus*; biotic vs. abiotic effects; Chile; competition; degu; *Octodon degus*; *Phyllotis darwini*; predation; foraging; small mammals.

INTRODUCTION

Small mammals rarely die of old age; most struggle to gather food resources before these are co-opted by other individuals, and ultimately succumb to predation. Consequently, it is widely accepted that understanding competition and predation is fundamental to understanding the autecology and community ecology of small mammals (e.g., Kotler and Holt 1989, Chase et al. 2002). The degree to which these biotic factors influence foraging may be modified by environmental factors such as season, lunar phase, microhabitat, and thermal regime (e.g., Kotler 1984, Brown 1988, Brown et al. 1988, 1994b, Mitchell and Brown 1990, Kotler et al. 1993, Hughes et al. 1994, Meyer and Valone 1999). Nonetheless, few investigators have addressed how the relative importance of biotic factors such as

competition and predation may vary under different abiotic conditions. This likely reflects the large effort required by studies of the foraging ecology of small mammals, especially when conducted across multiple seasons, lunar phases, or years with markedly different climatic conditions.

A key approach to understanding foraging behavior in natural conditions is the use of artificial foraging stations, which allow researchers to quantify foraging effort under different conditions. In recent years, four research groups have quantified foraging effort with giving-up densities (GUDs), the density of a resource at which foragers cease to exert additional effort. These studies have been conducted in arid regions in North America, Israel, southern Africa, and recently in South America. In the Sonoran Desert, Brown (1988, 1989a, b) pioneered the use of GUDs with his studies evaluating mechanisms of coexistence among four rodent species. Seasonal patterns in small-mammal demography and community structure were explained in terms

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of thermoregulatory costs, seasonal differences in predator (e.g., raptors vs. rattlesnakes) abundances (see also Kotler 1984, Meyer and Valone 1999), and spatial variation in resources. Subsequent work with Israeli gerbils (*Gerbillus pyramidum* and *G. allenbyi*) supported the importance of predation (Brown et al. 1994b, Kotler et al. 1994) and microhabitat partitioning (Brown et al. 1994a, Rosenzweig and Abramsky 1997). In the Namib Desert of southern Africa, Hughes et al. (1994) interpreted microhabitat-specific GUDs for gerbils (*Gerbillurus tytonis*) and a striped mouse (*Rhabdomys pumilio*) in terms of differential predator risk; both species preferred shrub habitat over open habitat, leading to shared habitat preferences and interspecific competition. Additionally, both species were less averse to using the open microhabitat under new moon conditions than full moon conditions, suggesting an important role of predation in this system.

A fourth group, Yunger et al. (2002) noted that these studies employed surrogate measures of predation risk (e.g., lunar light levels, shrub cover). Yunger et al. (2002) studied foraging decisions by three species of Chilean rodents under conditions of experimental exclusion of predators (both aerial and terrestrial) and/or competitors in a factorial design, using a series of replicate grids at a semiarid scrubland site in northern Chile. These authors were able to quantify more clearly the influence of predation, competition, and the interaction of these factors on foraging decisions by small mammals at their site.

Yunger et al. (2002) reported that predation influenced all three species, although this was not always the dominant influence. Diurnal *Octodon degus* foraged more under shrubs and where predators had been excluded, but no significant interaction was found between predator exclusion and microhabitat, indicated that foraging in "open" microhabitat did not increase when predators were excluded, and that thermoregulatory constraints, and not predation, limit foraging in open areas by this species (see Lagos et al. 1995). Foraging by nocturnal *Phyllotis* also was influenced by predators, although less so than *Octodon*, but it also foraged more in open microhabitats than under shrubs, evidently reflecting resource depletion under shrubs by the larger and competitively dominant *Octodon*. The third and smallest species, *Akodon* (nocturnal), was the least efficient forager at this site, and foraged most extensively in the absence of both competition and predation.

A limitation of most of the above studies is that the temporal duration was relatively brief, thus lacking the ability to assess the effects of population size and time (e.g., season, year) on foraging strategies. Yunger et al. (2002) manipulated predator and competitor numbers, but their study was restricted to a brief period in the austral summer (January) of 1993. Environmental conditions at their site are known to vary greatly between summer and winter, including seasonal changes

in predators (e.g., some diurnal raptors are more abundant at Fray Jorge in winter than summer) and competitors (e.g., many bird species at Fray Jorge summer in southern Chile and Argentina or in the Andes). Additionally, many small-mammal populations undergo seasonal and multiyear fluctuations in numbers, and community composition at many sites may vary temporally as well (Meserve et al. 1996, 1999, 2003). Finally, large-scale environmental perturbations, such as El Niño Southern Oscillations (ENSO), may result in dramatic changes in the relative abundances of various community members (e.g., Meserve et al. 1995, 1999, Jaksic et al. 1997, Jaksic 2001). ENSO affects primary productivity in many arid regions (Brown et al. 1997, Polis et al. 1997, Gutiérrez et al. 2000, Jaksic 2001), including the site studied by Yunger et al. (2002; see Meserve et al. 1995, 1999, 2003).

We extended upon the study by Yunger et al. (2002) by repeating a similar protocol over multiple seasons (summer vs. winter) and years (1999, 2000, 2001). We addressed similar questions to those posed by Yunger et al., namely, the role of microhabitat, lunar phase, and predation and competition, on foraging by three species of small mammals. Additionally, however, we added the temporal component of sampling over multiple seasons and years. Finally, since our study spanned periods of drought and abundant rainfall, we evaluated how seed predation varied with long-term changes in climate, which in this system, correlate well with small-mammal abundance.

METHODS

Research was conducted at Parque Nacional Bosque Fray Jorge (Fray Jorge), located ~400 km north of Santiago and 100 km south of La Serena, on the coast of northern Chile (30°41' S, 71°40' W, ~80 m elevation). Covering nearly 10 000 ha, this park constitutes the largest area of intact thorn scrub habitat in northern Chile, and is classified as coastal and forested steppe chaparral (*matorral estepario costero* and *matorral estepario boscoso*; Gajardo 1993). Parallel to the Pacific coast is a low range of hills (Altos de Talinay, ~650 m elevation), and just inland from this is the Quebrada de las Vacas, where our work was focused. Summers are warm (~25°C) and dry, and winters are mild (~21°C). Although this site receives little rainfall (~100 mm), there is some additional deposition from fog (*camanchaca*) due to adiabatic cooling on the coastal hills. Perhaps reflecting this, the vegetation is relatively dense (~50–60% shrub cover; Gutiérrez et al. 1993). Dominant plant species include *Porlieria chilensis*, *Proustia pungens*, and *Adesmia bedwellii*.

The small-mammal community here is rich and well documented (e.g., Meserve and Le Boulengé 1987, Meserve et al. 1995, and references therein), with ten species of widely differing habits. Meserve et al. (1999) classified these species as core, quasi-core, and opportunistic. Core species persist in the thorn scrub hab-

itat through all years of study, and include the herbivorous degu (*Octodon degus*; mass ~140 g), the herbivorous-granivorous Darwin's leaf-eared mouse (*Phyllotis darwini*; 58 g), and the insectivorous didelphid elegant fat-tailed opossum (*Thylamys elegans*; 23 g). The omnivorous olive grass mouse (*Akodon olivaceus*; 32 g), is generally present but considered a "quasi-core" species because it exhibits strong oscillations during and following El Niño events. Opportunistic species disappear from thorn scrub habitat in dry years, and include the granivorous long-tailed pygmy rice rat (*Oligoryzomys longicaudatus*; 24 g) and the insectivorous long-haired grass mouse (*Abrothrix longipilis*; 54 g). Two other species, Bennett's chinchilla rat (*Abrocoma bennetti*; 180 g) and the moon-toothed degu (*Octodon lunatus*; 150 g), are rare to sporadic in occurrence and are not considered here. All of these species are nocturnal except the degu, which is diurnal; at high densities *Akodon* and possibly *Oligoryzomys* extend their active periods to crepuscular and even diurnal hours.

The park has a diverse predator fauna including the culpeo fox (*Pseudalopex culpaeus*), the Burrowing Owl (*Speotyto cunicularia*), Great-horned Owl (*Bubo virginianus*), Barn Owl (*Tyto alba*), Bay-winged Hawk (*Parabuteo unicinctus*), Black-chested Buzzard-eagle (*Geranoaetus melanoleucus*), and Red-backed Hawk (Harris' Hawk [*Buteo polyosoma*]). Additionally, White-tailed Kites (*Elanus leucurus*) are present seasonally, and Cinereus Harriers (*Circus cinereus*) occur occasionally. Finally, two snakes (*Tachymenis chilensis* and *Philodryas chamissonis*) and a predatory lizard (*Callopistes paluma*) are found at Fray Jorge; the former likely are not influenced by our exclusions, but the latter has become substantially more abundant on predator exclusion than control grids (A. H. Minn, *personal communication*). Although this species could be responding to elevated small-mammal numbers in predator-exclusion grids, we believe this to be unlikely for three reasons. First, such a response would be nearly perfect compensation for the exclusion of endothermic predators, as neither *Akodon* nor *Phyllotis* have exhibited strong demographic responses to predator exclusion (Meserve et al. 2003). Second, culpeo foxes and some raptors in this region are known to consume lizards (Jaksic 1997, Jaksic et al. 1982), so it also is possible that *Callopistes* are responding to release from predation. Finally, since *Callopistes* is diurnal and *Phyllotis* and *Akodon* are largely or exclusively nocturnal, we have no reason to believe that *Callopistes* is influencing foraging decisions by these small mammals.

Sixteen permanent small-mammal trapping grids were installed in the austral winter of 1989, and were randomly allocated to one of four treatments with removal either of predators (avian and mammalian) and/or the large and behaviorally dominant rodent, the degu ($N = 4$ grids/treatment). A final four grids served as

controls and allowed access by all members of the community (for sampling and design details see Meserve et al. 1995, 1996, 1999, 2003).

Small-mammal foraging activity was evaluated with small aluminum trays ($21.6 \times 27.9 \times 5.1$ cm [width \times length \times height]) provisioned with 630 cm³ of fine sand and 30 g of non-hulled oat seeds (autoclaved to prevent germination). The density of seed used was extrapolated from earlier work (Yunger et al. 2002). Seed trays were put out in the morning prior to diurnal activity. At dusk, the sand was sieved to remove seed, and a fresh batch of 30 g of seeds was added. The mass of seed remaining represented the density of seed at which foraging was terminated, or the giving-up density (GUD) for the tray. Experiments were conducted for three consecutive days and nights except in the austral winter of 2001, when heavy rains forced us to terminate experiments after only two days and nights.

Our experimental unit was the replicate plot; we used 4 predator exclusions and 4 degu exclusions. Each plot was provisioned with 4 sets of 2 seed trays placed either under shrubs or in open microhabitat (≤ 1 m from shrub cover); 2 sets were placed inside the plot and 2 sets were placed in similar habitat outside (≤ 30 m) the plot. One tray in each set was housed in a hardware-cloth cage with a single large entrance leading to a 50-cm tube of 10.2 cm diameter polyvinyl chloride (PVC) pipe with a 90° angle to allow access by small mammals but deter birds. This method proved very successful, as we had only one documented case (plus one possible entrance) of a bird entering the seed trays. A second tray in each set was housed in a hardware-cloth cage with small holes (2.5 cm) cut in the sides to allow access by small mammals (e.g., *Akodon*, *Abrothrix*, *Oligoryzomys*), but exclude larger small mammals (e.g., degus, *Abrocoma*) and birds. We refer to these trays by the genus of small mammal whose foraging efforts are being evaluated. *Akodon* was the dominant small species throughout most of the study and all foraging in "small" trays is considered to reflect the activity of this species (see also Younger et al. 2002). Diurnal foraging in "large" trays was considered to reflect activities by *Octodon*, whereas nocturnal foraging in these trays was allocated to *Phyllotis*. As reported by Younger et al. (2002), trays accessible to large species had more extensive foraging, suggesting that *Akodon* were not depressing GUDs in trays to which larger taxa only had access, even though they had access to both small and large trays. Although *Akodon* is smaller than *Phyllotis*, we were not consistently able to distinguish footprints of these species.

We repeated all experiments under full and new lunar phases, allowing us to quantitatively evaluate the importance of lunar light levels on small-mammal foraging decisions. We repeated these experiments in summer and winter across three years (austral winter 1999 through austral winter 2001), allowing us to evaluate seasonal changes in foraging. Because small-mammal

TABLE 1. Classification variables used in rmANOVA in this study, including the nature of the variable (random vs. fixed), and a brief description of each variable.

Variable (nature)	Description
Plot (random)	Eight experimental plots with either degus ($N = 4$) or predators ($N = 4$) removed. This variable is not interpreted biologically, but was included because plots logically nest within treatment.
Tray (fixed)	“Large” or “small” trays: Large trays had large (~10 cm diameter) entrances with 50 cm long PVC pipe and a 90° angle to exclude birds, whereas small trays had small (2.5 cm diameter) openings cut in the hardware cloth to exclude larger rodents (e.g., degus, <i>Abrocoma</i>), as well as birds.
Microhabitat (fixed)	Under shrub cover vs. open habitat ≥ 1 m from shrubs
Treatment (fixed)	Codes for removal of degus or of predators; for logistical reasons we could not include plots where both degus and predators were excluded.
Degu or Predator (fixed)	Codes for trays that were inside vs. outside of mammal treatments (either degu or predator exclusions).
Time of Day (fixed)	Diurnal vs. nocturnal
Lunar Phase (fixed)	Full moon vs. new moon
Season (fixed)	Summer ($N = 2$) vs. winter ($N = 3$)
Year (fixed)	Three years of study, from austral winter 1999 through austral winter 2001. Not a variable of great interest per se, but this variable should be perceived as a surrogate for changes in small-mammal population sizes, which ranged from <50 in the austral winter of 2000 to >1300 in the winter of 2001.

populations changed substantially during the course of this study, we consider years of analysis to be a surrogate for small-mammal numbers. This would be a dangerous assumption if any other important variables changed across years. Indeed, precipitation and, presumably, primary productivity changed markedly in the third year of study. If this were to influence foraging in trays, however, we would expect foraging in trays to decrease in the face of elevated background food availability, and this is exactly the opposite of what we observed. For this study, small-mammal numbers were evaluated simply as the total number of individuals captured in the three-month period centered on the month of our fieldwork.

Thus, we employed a factorial design that allowed us to simultaneously compare the influence of predators, degus, microhabitat, lunar phase, and season for the three dominant small mammals at this site (Table 1). Additionally, because this study spanned a high rainfall event, we were able to evaluate how these patterns changed as small-mammal populations varied across an order of magnitude; although rainfall in 2000–2001 exceeded that in the ENSOs of 1991–1992 and 1997, the climatic events of 2000–2001 was not formally classified as an El Niño event.

Predictions

The large number of response variables evaluated here makes it difficult to outline predictions for all main effects and variable interactions. We have attempted to simplify this by restricting our analyses to three-way and lower interactions, but this leaves us with 7 main effects and 35 unique two- and three-way interactions. Some of these are not informative, such as comparing Time of Day (nocturnal vs. diurnal) for either the diurnal *Octodon* or the nocturnal *Phyllotis*. Additionally, there is little point in evaluating the role of degu ex-

clusion on foraging activity by degus. To make some sense of this, however, we outline general predictions for main effects and two-way interactions in Table 2 and in the following paragraph.

All species were expected to increase foraging activities when predators were excluded, although if *Akodon* interacted strongly with *Phyllotis*, it might show no response or even decreased activity in predator-exclusion trays (the latter species is larger and presumably the dominant competitor). Reflecting energetic and vigilance costs, all species were expected to forage more extensively in winter and under shrubs in both seasons. Nocturnal species (*Phyllotis* and *Akodon*) should forage more under new lunar phases, but this was not expected to influence the diurnal *Octodon*. *Akodon* should forage more at night than diurnally, reflecting its primarily nocturnal activity, and we expected the difference between nocturnal and diurnal foraging to be greater in summer than winter (thermal constraints) and in the absence of either predators or degus. Divergence in foraging effort between microhabitats should be greater under the full moon for nocturnal taxa (predator avoidance), and in winter for diurnal ones (thermoregulatory constraints), and should be reduced under predator exclusion but not under degu removal; for *Akodon* we expected this divergence to be reduced diurnally, as thermal constraints might limit foraging in open microhabitats. Differences across lunar phase were expected to be greater in the presence than absence of competitors or predators, but should not differ overall across seasons. Seasonal differences should be reduced in the exclusion of predators or degus. Finally, all factors should be influenced by population density, with more extensive foraging at high population numbers. Moreover, the divergence between such response variables as microhabitat, lunar phase, and season may be amplified during high-density pe-

TABLE 2. Outline of predictions for foraging activities by three species of small mammal at Fray Jorge, Chile.

Variable	<i>Octodon</i>	<i>Phyllotis</i>	<i>Akodon</i>
Direct effects			
Plot ($N = 8$)	n.a.	n.a.	n.a.
Tray (open, large hole, small hole)	n.a.	n.a.	n.a.
Degus	n.a.	+D < -D†	+D < -D†§
Predation	+P < -P‡	+P < -P‡	+P < -P‡§
Year (\approx population density)	2000 < 1999 < 2001†	2000 < 1999 < 2001†	2000 < 1999 < 2001†
Season	summer < winter†	summer < winter†	summer < winter†
Microhabitat	open < shrub†	open < shrub†	open < shrub†
Lunar Phase	full \approx new¶	full < new†	full \leq new†
Time of Day	n.a.	n.a.	diurnal \leq nocturnal‡
Interactions			
Year \times All other factors	2000 < 1999 < 2001¶	2000 < 1999 < 2001¶	2000 < 1999 < 2001¶
Season \times Microhabitat	summer > winter†#	summer \approx winter‡	summer \geq winter†
Season \times Lunar Phase	summer \approx winter‡	summer \approx winter‡	summer \approx winter‡
Season \times Time of Day	n.a.	n.a.	summer > winter†
Microhabitat \times Lunar Phase	full \approx new†	full > new‡	full > new‡
Microhabitat \times Time of Day	n.a.	n.a.	diurnal < nocturnal†
Microhabitat \times Predators	+P > -P‡	+P > -P‡	+P > -P‡§
Lunar Phase \times Time of Day	n.a.	n.a.	diurnal < nocturnal‡
Predation \times Time of Day	n.a.	n.a.	+P > -P‡
Predation \times Season	+P > -P‡	+P > -P‡	+P > -P‡
Predation \times Microhabitat	+P > -P‡	+P > -P‡	+P > -P‡§
Predation \times Lunar Phase	+P \approx -P†	+P > -P‡	+P \geq -P‡
Degu \times Time of Day	n.a.	n.a.	+D > -D‡
Degu \times Season	n.a.	+D > -D‡	+D > -D‡§#
Degu \times Microhabitat	n.a.	+D \approx -D†	+D \approx -D†
Degu \times Lunar Phase	n.a.	+D \approx -D†	+D \approx -D†

Notes: Inequalities indicate which treatment is expected to receive greater foraging effort; thus, e.g., for *Octodon*, predator-access (+P) trays should have less foraging than predator-exclusion (-P) trays, and the difference between microhabitats (open vs. shrub) is expected to be greater in summer than winter (e.g., summer > winter). Further abbreviations are: +D, degu-access treatment; -D, degu-exclusion treatment; n.a., not applicable.

† Predictions that were upheld by our data.

‡ Predictions that were not supported by our data.

riods, because we expected proportionally greater increases in foraging at “safe” foraging sites (e.g., under shrubs) than in sites perceived as dangerous (e.g., open microhabitats). This assumes that animals are not food stressed, as might occur when population size is declining in response to reduced food availability; in this study, however, we sampled before and during a period of high food availability, so we did not foresee any such complications.

Data analysis

Data initially were analyzed with a mixed-model repeated-measures analysis of variance (rmANOVA) with nine classification variables (Table 1), using SAS PROC GLM (version 8.2, SAS Institute, Cary, North Carolina, USA). All inference emphasized Type III sums of squares. Because interpretation rapidly becomes difficult with model complexity, we considered only main effects and second- and third-order interactions among these variables. We treated replicate plots as random variables, and all other factors as fixed. An additional problem with complex ANOVA models is that relatively small effects may yield statistically significant patterns that may be biologically trivial; this is because when evaluating one factor the analysis con-

trols for all other factors in the model. To avoid deceptive results, we plotted all significant effects to evaluate the nature of the interaction.

Initial results indicated that, as expected, different trays (e.g., those with small vs. large holes) received different levels of foraging, so we analyzed foraging separately by the three primary small mammals (*Akodon*, *Phyllotis*, *Octodon*). These analyses were affected with six-factor repeated-measures analyses of variance (rmANOVA), with fixed and random effects as in the preceding analysis.

Predators and degus also had different influences on foraging behavior. Whereas seed consumption was similar in degu and predator exclusions ($MS = 26$, $F = 0.31$, $P > 0.59$), it was significantly lower outside than inside treatments ($MS = 194$, $F = 7.45$, $P < 0.05$); the interaction between these variables was also significant ($MS = 297$, $F = 11.2$, $P < 0.02$), suggesting that small mammals responded differently to the removal of predators than to removal of degus. Consequently, and partially reflecting our a priori expectation of different responses to these two treatments, we treated these as separate experiments, analyzed as separate mixed-model rmANOVAs evaluating a single main effect (either Degus or Predators) and all second- and third-order

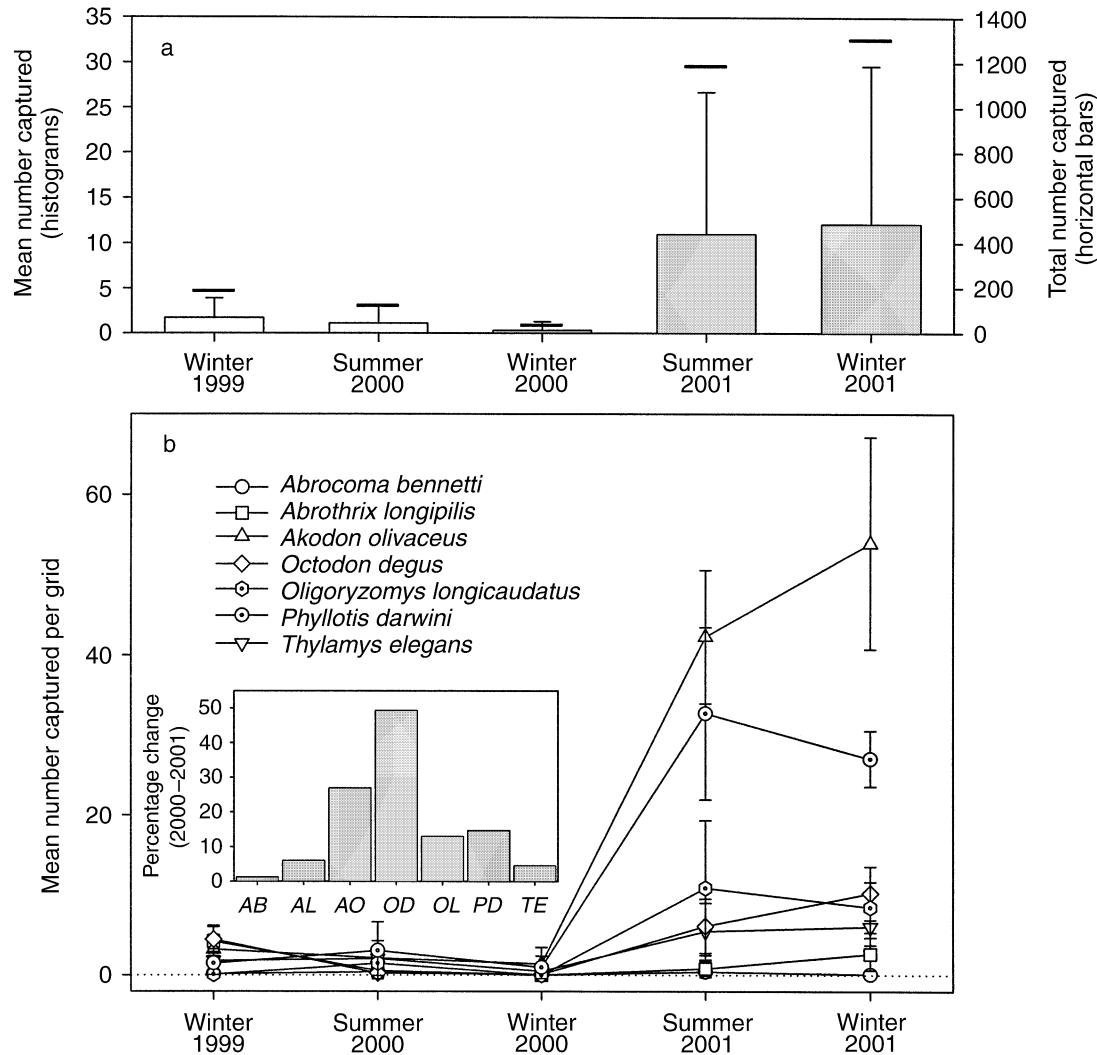


FIG. 1. (a) Mean (histogram bars) and total (horizontal bars) numbers of individual small mammals captured in four control plots during a three-month period centered on our foraging study. Error bars indicate ± 1 SD. Bars with similar fill (open vs. gray) are not significantly different. (b) Number of individuals (± 1 SD) captured in control plots during the three-month period bracketing our field sessions. The inset provides the increase between 2000 and 2001 (2001 captures/2000 captures) for each species (abbreviations are taken from the first letter of genus and species names).

interactions with this effect. The Plot main effect also was evaluated in order to incorporate variation among plots in the error terms.

Finally, for some three-way interactions involving year, we evaluated the nested two-way interactions for each year separately. This was done to discern the degree to which these were influenced by results from 2001, when small-mammal numbers were particularly high.

To summarize, we ran four sets of analyses. The first analysis included all data, evaluating the need for separate analysis of subsets of our data. We then evaluated control plots, predator exclusion, and degu exclusion separately. In all of these analyses we separated major foraging groups to evaluate how they were influenced by experimental factors.

RESULTS

Mammal populations changed significantly ($MS = 3580$, $F = 31.6$, $P < 0.0001$) during the course of this study (Fig. 1a). In the first three seasons of work, the number of captures on four control plots declined from 187 to 36 animals. Elevated precipitation led to a boost in primary productivity followed by increased numbers of small mammals, such that numbers in the final two seasons were ~ 1200 – 1300 individuals across four control plots. The greatest increases in 2001 (Fig. 1b) were by *Octodon* (~ 50 fold), *Akodon* (~ 27 fold), *Phyllotis* (~ 15 fold), and *Oligoryzomys* (~ 13 fold). Because these increases were expressed over differing initial numbers, they do not necessarily reflect densities in 2001, when the most abundant species (in declining

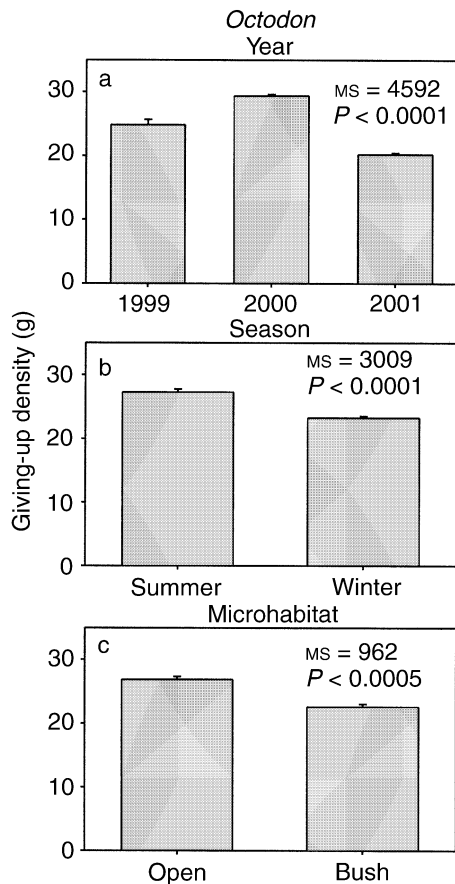


FIG. 2. Foraging by *Octodon degus* by year, season, and microhabitat under control conditions. Presented is the mean (+1 SD) mass of seed remaining after a 12-hour foraging period (i.e., giving-up densities); lower values reflect more intensive foraging. Summary statistics are provided. Results for *Phyllotis darwini* and *Akodon olivaceus* were qualitatively identical for these direct effects.

order) were *Akodon* and *Phyllotis*, followed by *Octodon*, *Oligoryzomys*, *Thylamys*, *Abrothrix*, and finally *Abrocoma* (Fig. 1b). To minimize the number of figures presented, several pairwise interactions are shown using figures of three-way interactions; thus, for example, Year \times Season effects for *Phyllotis* and *Akodon* are clearly visible in figures of Year \times Season \times Lunar Phase, and so the former are excluded.

Control trays

Octodon.—Foraging by degus was significantly influenced by year, season, and microhabitat (Table 3, Fig. 2). Foraging intensity was directly related to population size over time (Fig. 2a); consumption was moderate in 1999, declined in 2000, and then increased greatly in 2001. Foraging was more extensive in winter than summer (Fig. 2b), although this was entirely caused by substantial differences in 2001 (Fig. 3a). Consumption was greater under shrubs than in open microhabitats (Fig. 2c); although there was no differ-

ence between microhabitats in 2000; this difference was notable in 1999, and even more evident in 2001 (see Fig. 3d). There was a strong trend ($P < 0.072$) for greater divergence between bush and open microhabitats in winter than summer, due almost exclusively to patterns observed in 2001 (Fig. 3d). A significant interaction between Season and Lunar Phase (Fig. 3b) reflected a greater influence of lunar phase in winter (with foraging greater under the new moon; $MS = 465$, $F = 5.72$, $df = 1$, $P < 0.02$) than summer ($MS = 23$, $F = 0.98$, $df = 1$, $P > 0.30$). A significant three-way interaction between year, season, and lunar phase (Fig. 3c) was due to this Season \times Lunar Phase interaction; this result was not expected for this diurnal species. The magnitude of this effect evidently was related to population densities; at low numbers (2000) foraging was similar under both lunar phases, but at higher densities (1999, 2001) foraging was greatest under new lunar phases in winter, and under full lunar phases in summer. We are presently at a loss to explain this pattern.

Phyllotis.—Results for leaf-eared mice were qualitatively similar to those for degus (Table 3), with significant effects of year, season, and microhabitat; surprisingly, however, we did not detect a significant main effect for lunar phase. The pattern of these differences was identical to that observed for *Octodon*, with greater foraging in winter than summer, under shrubs than in the open, and declining overall from 1999 to 2000 before sharply increasing in 2001. Additionally, interactions between Year and both Microhabitat (Fig. 4a) and Season (see Fig. 4c) were qualitatively similar to those observed for *Octodon*, except that foraging activity for *Phyllotis* increased more in summer 2001 than for *Octodon*. The effect of moonlight was evidenced in significant interactions between Lunar Phase and both Season (Fig. 4b) and Year (see Fig. 4c), driven largely by data from 2001; whereas foraging under the full moon was similar in both seasons in 2000, it increased greatly in winter 2001 (Fig. 4c).

Akodon.—Patterns of foraging by *Akodon* paralleled those of *Octodon* and *Phyllotis*, with significant effects of year, season, and microhabitat (Table 3). In three of five seasons, there was a trend for diurnal foraging to be more extensive than nocturnal foraging (Fig. 5d); this was offset in summer 2001 by greatly increased nocturnal foraging, such that overall diurnal foraging was not greatly different than nocturnal foraging ($P < 0.03$, but with a very low MS and only 0.25 g difference in seed consumed). As predicted, the difference in foraging effort between microhabitats was greater nocturnally than diurnally. Interactions between Year and both Season and Microhabitat were similar to those outlined for *Octodon* and *Phyllotis*, and that between Season and Lunar Phase (Fig. 6a) was intermediate to the diurnal *Octodon* and nocturnal *Phyllotis*, with similar foraging under both lunar phases in summer, but greater foraging in winter under a new moon; as with *Phyllotis*, this

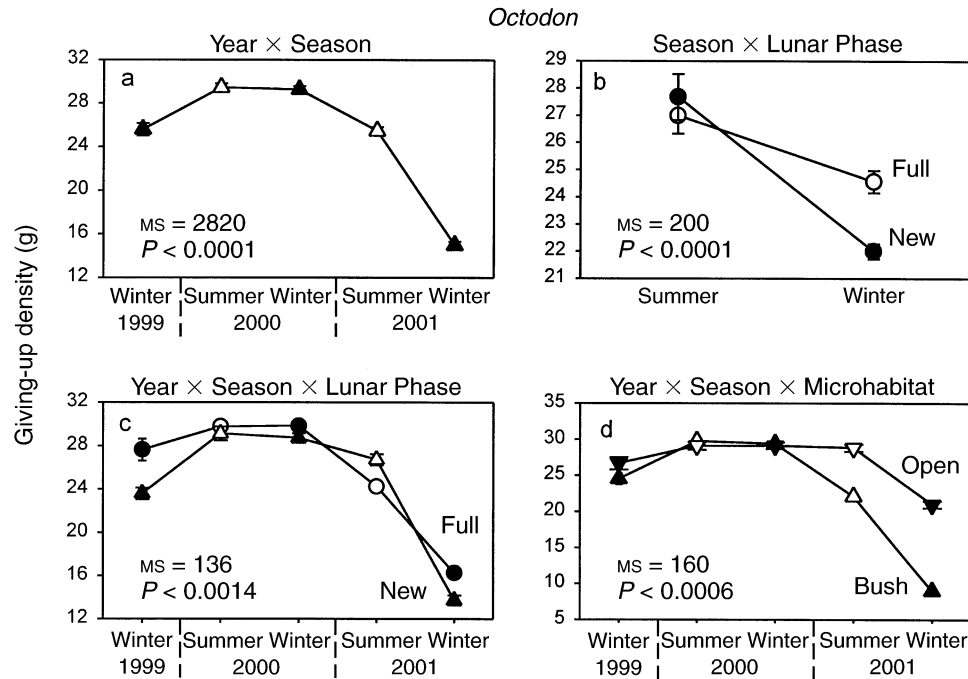


FIG. 3. Foraging by *Octodon degus* under control conditions. Presented is the mean (± 1 SD) mass of seed remaining after a 12-hour foraging period (i.e., giving-up densities), with associated summary statistics, for significant effects.

difference was due entirely to relatively low foraging in winter 2001 under full moon conditions.

Although foraging was greater under shrubs than in the open, this difference was significantly greater in winter, reflecting much greater foraging under shrubs in this season (Fig. 6b); this was similar to the pattern observed for *Octodon*, and reflected differences found only in 2001 (Fig. 5b). As expected, foraging under shrubs was greater at night than during the day, whereas nocturnal and diurnal foraging was similarly low in open trays (Fig. 6c).

Mirroring patterns for *Octodon* and *Phyllotis*, three-way interactions were dominated by interannual differences, likely reflecting changes in *Akodon* numbers at the site (Fig. 1b). In addition to patterns outlined in this section, foraging in open microhabitat was similar during nocturnal and diurnal periods for both summer and winter; during the summer, however, foraging under shrubs was substantially greater than during the day (Fig. 5c). Finally, foraging generally was greater under the new than the full moon (Table 3), but nocturnal foraging in summer by was not significantly different under both lunar phases (Fig. 5a).

Exclusion of predators

No species foraged significantly more in the absence of predators (Table 4). Nonetheless, for *Phyllotis* and *Akodon* there were some interesting trends across predator treatments. In general, responses observed in control trays were mildly amplified under the exclusion of predators.

Phyllotis.—Two three-way interactions suggested that predators indirectly influenced foraging by this species. First, a significant interaction between Year and Microhabitat ($MS = 1579$, $P = 0.0003$) was mildly amplified by predators (Fig. 7a). Although this interaction appears to be driven by the nested Year \times Microhabitat interaction, there also was a strong but not significant interaction between Microhabitat and Predator access in 2001 ($MS = 147.28$, $F = 3.21$, $P < 0.075$; Fig. 7a); foraging in open areas was somewhat greater in the absence of predators, but these were roughly similar under shrub cover.

Second, a significant Season \times Lunar Phase interaction was magnified across predator treatments (Fig. 7b). Under a new moon, trays experienced greater foraging effort in winter than summer, whereas foraging either was similar (predator-access trays) or was significantly reduced (predator-exclusion trays) under a full moon.

Akodon.—A significant Season \times Lunar Phase interaction ($MS = 617$, $P < 0.005$) was amplified across predator treatments (Fig. 7c). In summer, all trays had similar levels of foraging ($P = 0.093$), but we recorded a significant interaction between lunar phase and predator treatment in winter ($MS = 190$, $F = 15.29$, $P < 0.03$); predator-free trays experienced greater foraging under new moon conditions, but under the full moon predator access trays received greater foraging. In fact, under a full moon predator-exclusion trays did not change substantially between seasons, unlike other treatments.

TABLE 3. Results of rmANOVAs on foraging effort for three rodent species for control trays only at Fray Jorge Forest National Park, Chile.

Source	df	<i>Octodon</i>			<i>Phyllotis</i>			<i>Akodon</i>		
		MS	F	P	MS	F	P	MS	F	P
Plot	7	43	0.49	0.8208	61	1.40	0.4145	45	-3.35	<0.0001
Year	2	4592	53.49	<0.0001	5855	97.07	<0.0001	4423	71.12	<0.0001
Season	1	3009	74.62	<0.0001	462	11.94	0.0104	1989	58.16	0.0001
Time of Day	1	54	7.51	0.0291
Lunar Phase	1	102	2.90	0.1396	36	2.00	0.2148	21	7.62	0.0878
Microhabitat	1	962	35.95	0.0005	1852	84.04	<0.0001	1898	50.47	0.0002
Year × Season	1	2820	149.42	<0.0001	464	16.99	0.0044	1841	40.69	0.0004
Year × Lunar Phase	2	31	1.40	0.2794	175	5.80	0.0144	92	6.01	0.0129
Season × Lunar Phase	1	200	96.73	<0.0001	665	46.52	0.0002	348	24.16	0.0017
Year × Microhabitat	2	1376	55.10	<0.0001	1918	57.67	<0.0001	3213	70.38	<0.0001
Season × Microhabitat	1	216	4.49	0.0715	52	3.45	0.1047	1245	23.73	0.0018
Year × Time of Day	2	254	32.85	<0.0001
Season × Time of Day	1	487	48.30	0.0002
Time of Day × Microhabitat	1	172	11.22	0.0057
Year × Season × Lunar Phase	1	136	10.30	0.0014	689	48.39	<0.0001	441	45.36	<0.0001
Year × Season × Microhabitat	1	160	12.08	0.0006	33	2.31	0.1294	946	97.36	<0.0001
Year × Season × Time of Day	1	398	40.91	<0.0001
Season × Time of Day × Lunar Phase	1	166	17.09	<0.0001
Season × Time of Day × Microhabitat	1	375	38.62	<0.0001

Notes: Summary statistics are presented for all main effects and for all analyses that appeared biologically meaningful; plot interactions are not included. Bold font highlights significant results ($P < 0.05$).

Exclusion of degus

In contrast to the limited response to predator treatments, both *Phyllotis* and *Akodon* responded significantly to degu exclusion (Table 5). Additionally, we recorded several significant interactions between degu removal and other measured variables.

Phyllotis.—Foraging by *Phyllotis* was greater in the absence of degu (Table 5, Fig. 8a; although this was due entirely to observations made in 2001 [Fig. 8b]), when foraging was significantly greater inside degu-exclosure grids in 2001 ($MS = 976$, $P < 0.03$ and MS

< 0.20 , $P > 0.40$ for 1999 and 2000, respectively). Significant three-way interactions generally reinforce interpretations from pairwise interactions, further underscoring the influence of data from 2001. Thus, foraging effort in open microhabitats generally increased under the new moon and in the absence of degu, but foraging under shrubs remained constant under new lunar conditions regardless of degu presence or absence (Fig. 8c). Finally, a significant interaction between Year and Microhabitat ($MS = 1101$, $F = 31.89$, $P < 0.0005$) was amplified across degu treatments; whereas trays

TABLE 4. Results of rmANOVAs on foraging effort for three rodent species for predator-removal trays only at Fray Jorge Forest National Park, Chile.

Source	df	<i>Octodon</i>			<i>Phyllotis</i>			<i>Akodon</i>		
		MS	F	P	MS	F	P	MS	F	P
Plot	3	8	0.07	0.9753	132	14.55	0.9470	39	2.58	0.8478
Predator treatment (Pred)	1	14	0.32	0.6116	4	0.83	0.4215	0	0.01	0.9438
Year × Pred	2	3	0.07	0.9326	4	0.36	0.7080	2	0.10	0.9051
Season × Pred	1	4	0.21	0.6805	12	1.19	0.3535	14	1.67	0.2846
Time of Day × Pred	1	6	0.49	0.5044
Lunar Phase × Pred	1	37	2.06	0.1891	8	0.42	0.5401	0	0.00	0.9856
Microhabitat × Pred	1	46	2.30	0.1814	24	0.46	0.5363	5	0.13	0.7406
Year × Season × Pred	1	8	0.56	0.4556	18	1.38	0.2414	43	4.04	0.0447
Year × Time of Day × Pred	2	1	0.11	0.8935
Season × Time of Day × Pred	1	17	1.60	0.2057
Year × Lunar Phase × Pred	2	40	2.71	0.0677	46	3.50	0.0310	27	2.48	0.0843
Season × Lunar Phase × Pred	1	19	1.32	0.2509	93	7.13	0.0079	182	16.98	<0.0001
Time of Day × Lunar Phase × Pred	1	2	0.14	0.7069
Year × Microhabitat × Pred	2	41	2.83	0.0604	41	3.12	0.0451	28	2.57	0.0772
Season × Microhabitat × Pred	1	34	2.33	0.1279	22	1.66	0.1982	39	3.61	0.0577
Time of Day × Microhabitat × Pred	1	1	0.14	0.7084
Lunar Phase × Microhabitat × Pred	1	9	0.62	0.4301	6	0.44	0.5096	32	2.95	0.0862

Notes: Presented are summary statistics for all main effects and for all analyses that appeared biologically meaningful; plot interactions are not included. Bold font highlights significant results ($P < 0.05$).

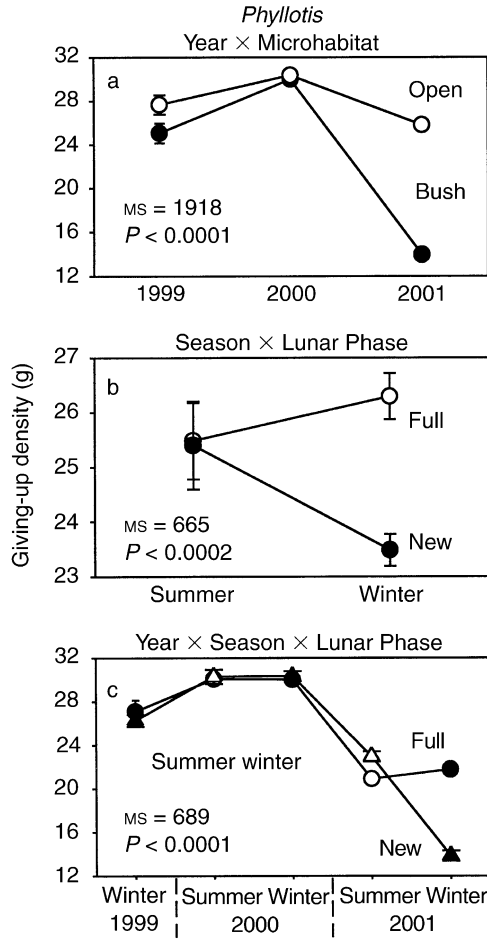


FIG. 4. Foraging by *Phyllotis darwini* under control conditions. Presented is the mean (± 1 SD) mass of seed remaining after a 12-hour foraging period (i.e., giving-up densities), with associated summary statistics, for significant effects.

under shrub cover experienced uniformly elevated levels of foraging in 2001, open trays under degu-exclusion treatments experienced much greater increases in foraging effort than those under degu-access treatments (Fig. 8d). These data all suggest that *Phyllotis* foraging increases in the absence of degus, although it is important to recall that this occurred against a background increase of $\sim 15\times$ in *Phyllotis* numbers between 2000 and 2001.

Akodon.—*Akodon* foraged significantly more in the absence of degus (Table 5, Fig. 8e); as with *Phyllotis*, this difference reflected differences in the third year of study (Fig. 8f). The three-way interaction between lunar phase, microhabitat, and degu treatment was significant (Fig. 8g) and reflected different responses to lunar phase in the presence and absence of degus. In the presence of degus, we recorded a significant interaction between moon and microhabitat (MS = 147, $F = 16.23$, $P < 0.03$); foraging in open microhabitats was similar in both lunar phases, but foraging under shrubs was much greater under a new than a full moon. In contrast, in the absence of degus there was no such interaction ($P > 0.8$), and lunar phases had similar influence on foraging in open and shrub microhabitats (Fig. 8g).

DISCUSSION

Our data agree in general, but differ in detail, with those reported by Yunker et al. (2002). Specifically, responses to biotic treatments are rather different in these two studies. These differences may be partially explained by differences in methodology, but we believe that comparisons between these two studies underscore the dynamic nature of this system. The most notable methodological difference is the greater duration of the present study (2.5 years vs. one month).

TABLE 5. Results of rmANOVAs on foraging effort for two rodent species for degu-removal trays only at Fray Jorge National Park, Chile.

Source	df	<i>Phyllotis</i>			<i>Akodon</i>		
		MS	F	P	MS	F	P
Plot	3	44	-1.69	<0.0001	19	-0.09	<0.0001
Degu treatment (Degu)	1	192	15.32	0.0247	342	11.44	0.0398
Year × Degu	2	209	9.93	0.0102	346	6.66	0.0286
Season × Degu	1	70	2.07	0.2449	200	9.42	0.0535
Time of Day × Degu	1	20	0.69	0.4500
Lunar Phase × Degu	1	54	2.58	0.1504	13	0.93	0.3597
Microhabitat × Degu	1	40	1.28	0.3135	34	0.38	0.5784
Year × Season × Degu	1	17	1.08	0.3001	36	2.63	0.1054
Year × Time of Day × Degu	2	21	1.52	0.2200
Season × Time of Day × Degu	1	1	0.07	0.7923
Year × Lunar Phase × Degu	2	44	2.74	0.0655	18	1.30	0.2725
Season × Lunar Phase × Degu	1	3	0.16	0.6861	51	3.68	0.0555
Time of Day × Lunar Phase × Degu	1	3	0.23	0.6344
Year × Microhabitat × Degu	2	68	4.22	0.0153	1	0.05	0.9473
Season × Microhabitat × Degu	1	18	1.12	0.2909	0	0.00	0.9784
Time of Day × Microhabitat × Degu	1	2	0.15	0.6980
Lunar Phase × Microhabitat × Degu	1	93	5.79	0.0165	89	6.43	0.0114

Notes: Presented are summary statistics for all main effects and for all analyses that appeared biologically meaningful; plot interactions are not included. Bold font highlights significant results ($P < 0.05$).

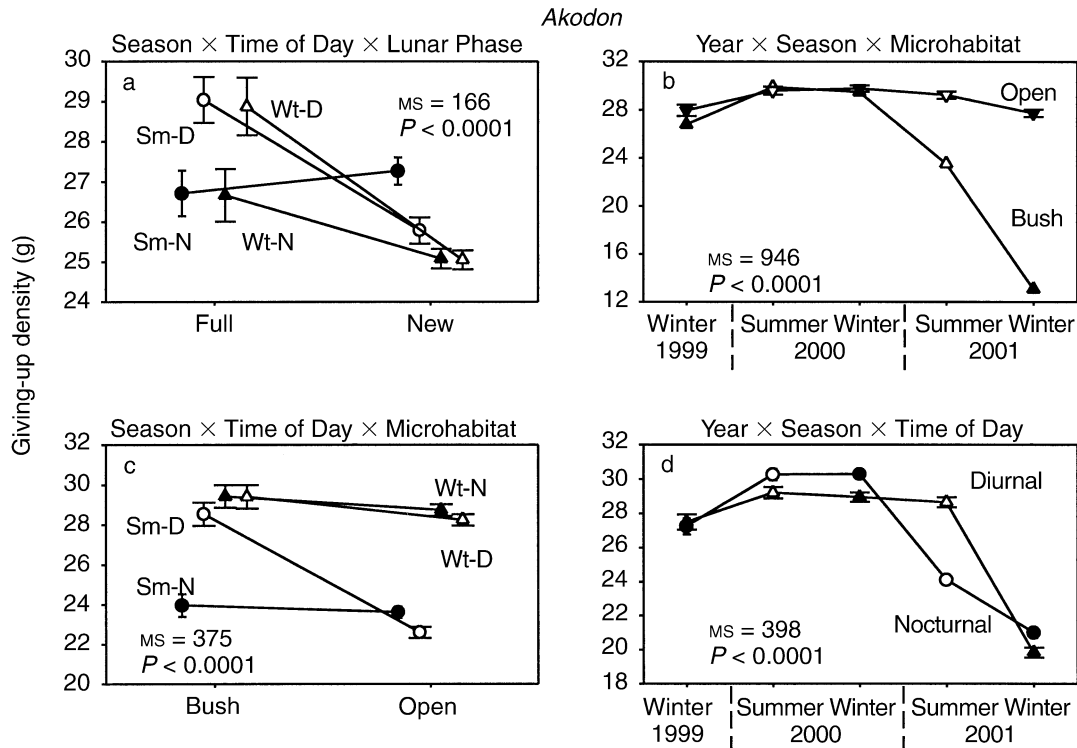


FIG. 5. Foraging by *Akodon olivaceus* under control conditions. Presented is the mean (± 1 SD) mass of seed remaining after a 12-hour foraging period (i.e., giving-up densities), with associated summary statistics, for significant three-way effects. Abbreviations are: Sm-D, summer, diurnal; Sm-N, summer, nocturnal; Wt-D, winter, diurnal; Wt-N, winter, nocturnal.

Additionally, however, we used separate cages to house feeding trays, and our feeding trays were larger, which we believe represented more natural foraging conditions than in Yunker et al. (2002). By spanning a longer period of time, this study was better able to represent the temporal heterogeneity (both seasonal and inter-annual) that characterizes this system. Small-mammal numbers at this site fluctuate dramatically over time (Meserve et al. 1995, 2003), and many other members of the Fray Jorge ensemble exhibit seasonal changes in abundance (e.g., many birds here are migratory and spend the austral summer in the Andes, in southern Chile, or in Argentina). It is particularly notable that the period of our observations spanned periods of both very low and high small-mammal populations.

Control conditions

Although most main effects significantly influenced foraging activity by all three species, lunar phase surfaced as a significant factor only in combination with other variables such as season, microhabitat, and year. This is not surprising, as lunar phase would be expected to influence activity more in open than covered microhabitats, and likely under high vs. low population density as well (e.g., see Kotler et al. 1993, Hughes et al. 1994, Vásquez 1994, Sutherland and Predavec 1999). Additionally, nocturnal and diurnal foraging differed significantly for *Akodon*, as expected. If year is a useful

proxy for mammal population size, then this appears to be the greatest single influence on foraging effort; across three years of study, foraging was monotonically related to population sizes for all three species. This seems a reasonable assumption; deer mice (*Peromyscus maniculatus*) in Canada also demonstrated clear density dependent foraging, with more extensive foraging at higher population density (Davidson and Morris 2001). Foraging intensity also was greater in winter than summer in all trays, and under the cover of shrubs than in open microhabitats, as observed elsewhere (e.g., Brown 1989b, Brown et al. 1994a, b, Hughes et al. 1994, Meyer and Valone 1999, Yunker et al. 2002). Moreover, many pairwise and three-way interactions were based on dynamics that occurred only in the final year of study. This was particularly clear for *Akodon*; with increasing numbers in summer and winter 2001, foraging was proportionally much greater under shrubs than in the open (Fig. 5b), and under a new moon relative to the full moon.

A second factor that had a strong and consistent influence on foraging activity was season (winter > summer; Table 3), likely reflecting either thermoregulatory constraints or the longer period available for nocturnal foraging in winter relative to summer. Again, however, this seasonal effect was due primarily to the very extensive foraging in winter 2001 (Fig. 3a). Finally, all species foraged more extensively under vegetative cov-

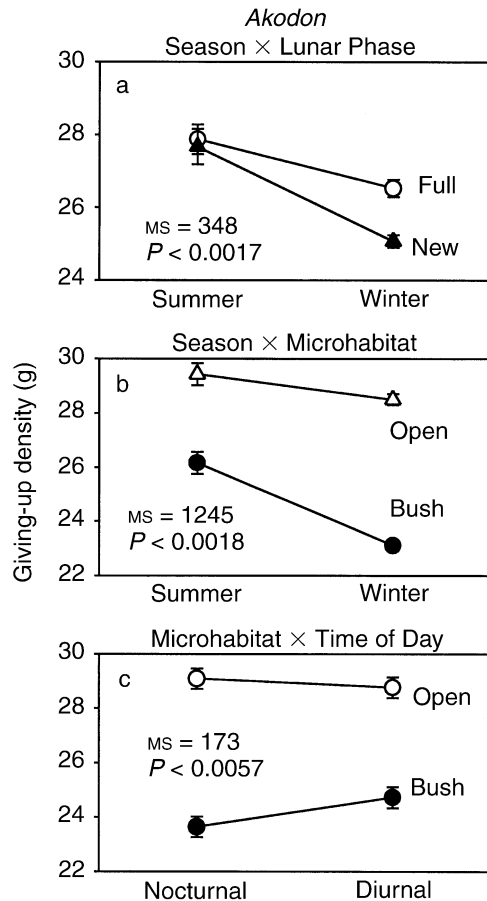


FIG. 6. Foraging by *Akodon olivaceus* under control conditions. Presented is the mean (± 1 SD) mass of seed remaining after a 12-hour foraging period (i.e., giving-up densities), with associated summary statistics, for significant two-way effects.

er (Table 3). This also was monotonically related to population size, however (Figs. 3d, 4a, and 6b).

Biotic factors

Whereas Yunker et al. (2002) reported substantial responses to predation, they found relatively limited responses to the experimental exclusion of degus. In contrast, we found much greater responses to the exclusion of degus than to that of predators.

Predators.—Yunker et al. (2002) reported that all three focal species foraged more in predator-exclusion grids, and that degus foraged more extensively under shrubs than in open microhabitats, but did not increase use of open microhabitat in the absence of predators. Moreover, predation threat reduced foraging by *Phyllotis*, whereas *Akodon* actually reduced foraging efforts in predator-exclusion plots, likely reflecting interference competition with the larger *Octodon* and *Phyllotis*. *Phyllotis* and *Akodon* both foraged more intensively under shrub cover, but neither species displayed significant interaction between microhabitat and predator

exclusion. *Akodon* foraged more at night than during the day, and the difference between predator-access and predator-exclusion trays was greatest at night. In contrast, Yunker et al. (2002) reported that predators had little effect on the nocturnal *Phyllotis*, based on limited response to predator removal and to activity patterns under full and new lunar phases.

In contrast to Yunker et al. (2002), our study did not elicit significant effects of predators (Table 4). For *Phyllotis*, microhabitat had a substantially greater influence on foraging than predation (Fig. 7a). Both *Phyllotis* and *Akodon* presented unexpected and rather inexplicable responses to lunar phase across predation

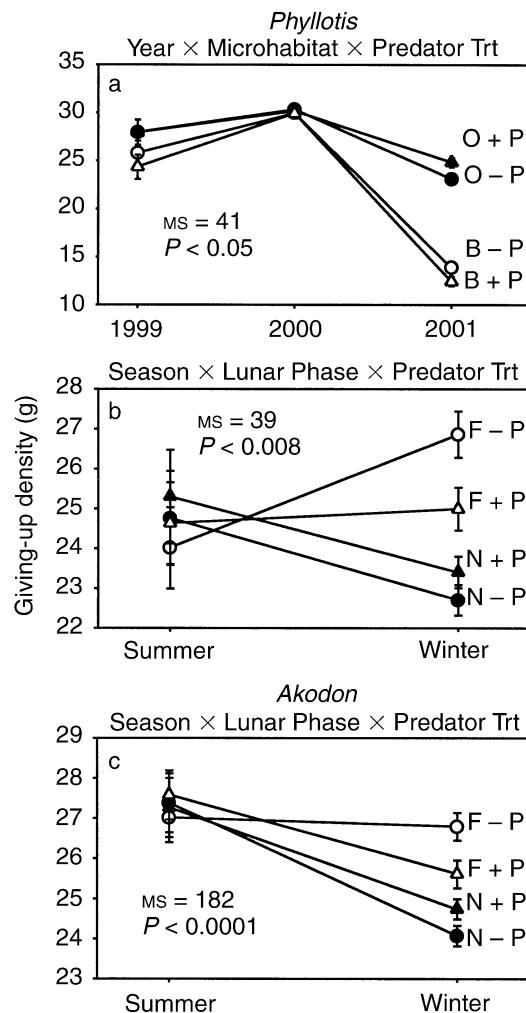


FIG. 7. Foraging by *Phyllotis darwini* and *Akodon olivaceus* across predator treatments. Presented is the mean (± 1 SD) mass of seed remaining after a 12-hour foraging period (i.e., giving-up densities), with associated summary statistics, for all significant effects. Abbreviations are: O+P, open microhabitat, predator access; O-P, open microhabitat, predator exclusion; B+P, bush microhabitat, predator access; B-P, bush microhabitat, predator exclusion; F+P, full moon, predator access; F-P, full moon, predator exclusion; N+P, new moon, predator access; N-P, new moon, predator exclusion.

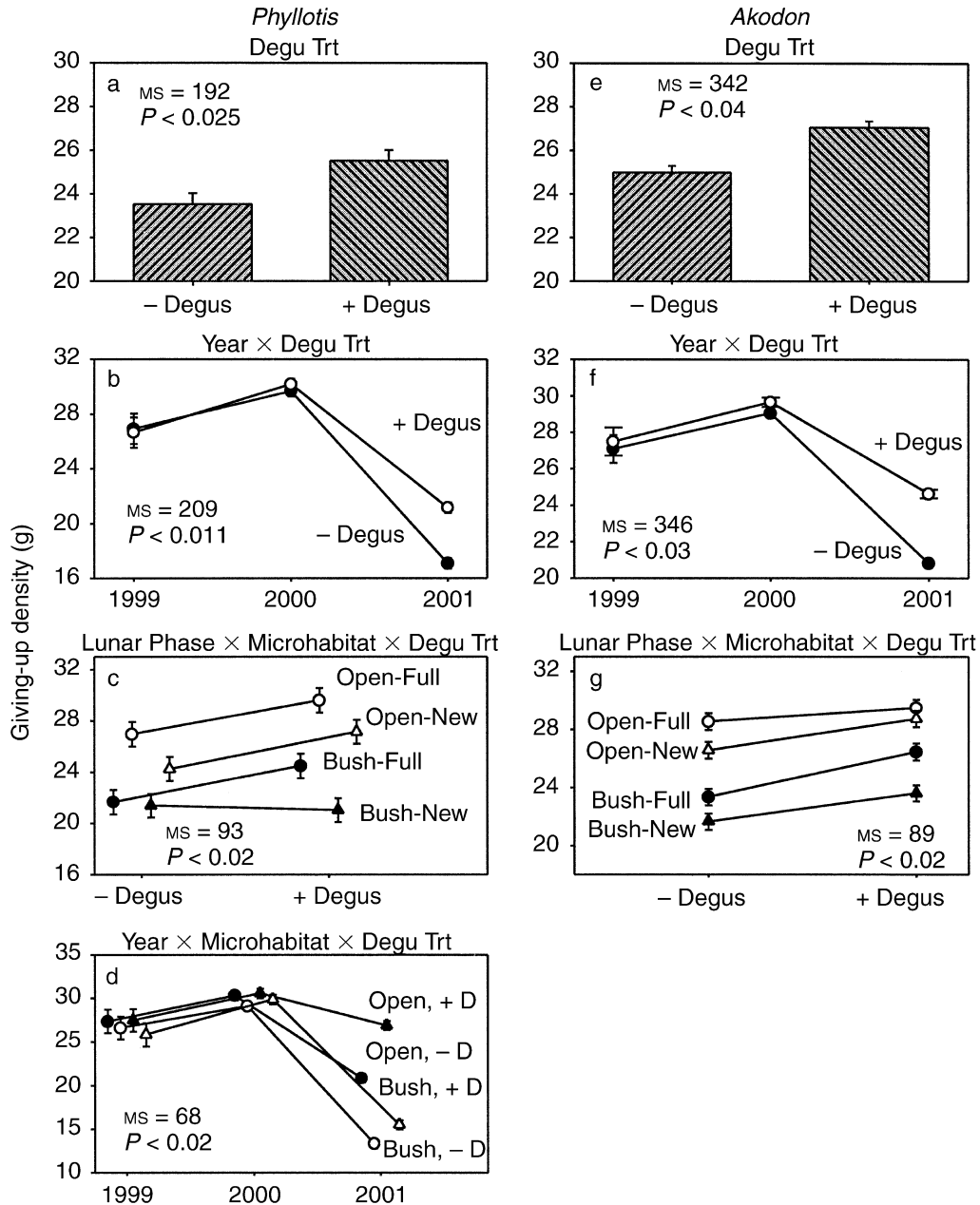


FIG. 8. Foraging by *Phyllotis darwini* and *Akodon olivaceus* across degu removal treatments. Presented is the mean (± 1 SD) mass of seed remaining after a 12-hour foraging period (i.e., giving-up densities), with associated summary statistics, for significant main effects as well as two- and three-way interactions.

treatments (Fig. 7b, c). All treatments were similar during summer months, but foraging during winter was greater under the new moon than under the full moon. To our surprise, however, foraging under a full moon was more intensive in the presence of predators (compare F - P and F + P in Fig. 7b, c), but the influence of predators was reversed under the new moon (compare N - P vs. N + P); consequently, in winter, the least and most intensive foraging was recorded in predator-free trays. These patterns might be explained if predator

numbers differ seasonally. At Fray Jorge, some aerial predators occur at lower number in the park during winter (e.g., White-tailed Kite and Cinereus Harrier, although neither are ever abundant in the park), and numbers of culpeo foxes appeared to be lower during our study than in 1993 when Yunger et al. (2002) conducted fieldwork (P. L. Meserve, *personal observation*), although neither observation has been quantified. An alternative explanation involves changes in methodology; the larger feeding trays in our study may measure trade-

offs between foraging gains and predation threat differently than the trays used by Yunger et al. (2002).

Degus.—Yunger et al. (2002) noted only one significant response to degu exclusion: *Akodon* foraged more in the absence of degus than in their presence, in part reflecting increased *Akodon* populations where degus were removed. They found no significant interactions, and no effects at all for *Phyllotis* (which also increased numerically when degus were removed).

We found the influence of *Octodon* to be more pervasive, and to be greatest in 2001, when small-mammal numbers were highest (Fig. 8b, f). In the absence of degus, *Phyllotis* increased foraging in all conditions except under shrubs and a new moon, when foraging was independent of degu presence or absence (Fig. 8c). These observations suggest that predator threat (full moon) has a greater influence on foraging by this species than does competition with degus.

Akodon foraging was elevated under all conditions of degu exclusion. Whereas the response to shrub cover was similar in both lunar phases when degus were excluded, this was rather limited in open microhabitats, but substantial under shrubs, when degus were present (Fig. 8g). Thus, degu influence foraging by *Akodon*, but this influence is highly contextual, depending both on microhabitat and lunar phase. As both of these factors may be useful surrogates for predator pressure, competition and predation both appear to influence foraging by this species, but this response is complex.

Synthesis

Perhaps more than anything else, these data underscore the importance of an adequate time scale in the analysis of responses to biotic and abiotic effects. The degree of granivorous foraging varied substantially over time, and a snapshot in any individual season or year would have missed much of the dynamics that characterize the system. In particular, the degree to which predation and competition influence the autecology of component species varied greatly with changing local demography; this, in turn, is driven largely by climatic patterns (Meserve et al. 2003). ENSO events significantly alter the landscape at Fray Jorge, increasing available moisture to arid-adapted plants and leading to significant increases in both vegetative and reproductive productivity (Gutiérrez et al. 1997). Our data provide conflicting insights to the relative importance of predation and competition on foraging decisions by these species. In contrast to earlier work at this site (Yunger et al. 2002), our results were equivocal about the role of predation at these sites, perhaps reflecting temporal fluctuations in population sizes or differences in methodology. In contrast to the lack of direct effects, however, indirect patterns strongly support the hypothesis that predation influences foraging decisions by all three species. Nonetheless, no species exhibited significant interactions between either microhabitat or lunar phase and the exclusion of

predators, suggesting either that predation is not influencing foraging decisions or that these animals do not recognize the protection from predators that is afforded by our exclusions.

On the other hand, our data indicate that competitive interactions strongly influence foraging decisions by *Phyllotis* and *Akodon*. Both species foraged significantly more in the absence of degus, especially in the third year of study when populations were high. Significant interactions between degu exclusion and both lunar phase and microhabitat, however (e.g., Fig. 3c, d), indicated that the effect of competition differed depending on the threat of predation. Further work should aim to further quantify this and to resolve contradictions between this study and that of Yunger et al. (2002; e.g., the relative influence of competition and predation).

Patterns of seed predation by small mammals are far from simple. While some generalities appear forthcoming (e.g., the role of shrub cover and lunar phase), the relative influence of biotic factors remain unresolved. Indeed, the relative importance of these factors in this study differ from that reported from the same site by Yunger et al. (2002). Discrepancies between our data and those of Yunger et al. (2002) suggest that the extent to which these animals respond to predator exclusion is variable over time. There likely is a lag between establishing residency on a predator-exclusion grid and recognizing that predation is no longer a substantial threat locally. Given that demographic increases on experimental plots during ENSO events generally are fueled by immigration, it might be expected that populations during and soon after ENSO events would retain high levels of vigilance; a corollary to this is that longer term residents should exhibit less vigilance on these experimental grids. Although our data are not supportive of this hypothesis, both this study and that of Yunger et al. (2002) occurred during or soon after periods of high precipitation, when immigration likely was higher than during intervening dry periods; only further work can address this point. In any event, the influence of competition and predation was dramatically less than that of environmental attributes such as shrub cover, season, and lunar phase, as has been demonstrated for most demographic variables (Meserve et al. 1993, 1995, 1996, 2003). In many respects, ENSO re-sets the ecological clock in arid and semiarid regions such as northern Chile (see also Jaksic 2001), altering population and community structure, predator densities and diets, and the nature and strength of factors driving or influencing demographic and behavioral characteristics of these taxa. Understanding the relative importance of biotic and abiotic factors on foraging and other behavioral decisions requires long-term observations. The application of fine-scale foraging experiments within well-replicated, long-term biotic manipulations illustrates the importance of such approaches for yielding insights to behavior and foraging strategies in variable environments.

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