

## Effect of plant cover on seed removal by rodents in the Monte Desert (Mendoza, Argentina)

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**Abstract** In desert areas, predation risk is one of the highest costs of foraging and is a major influence on animal behaviour. Several strategies are used by foragers for surviving and reproducing in desert areas. The foraging strategies of the small mammals of South American deserts are still poorly known. In this study, we investigated the foraging strategies of rodents of the Monte Desert in response to distance from seed sources to sheltered sites (i.e. shrubs) during two different seasons (wet and dry). We evaluated the relative rates of removal of two species of seeds (millet and sunflower) by rodents at two sites by establishing 80 seed sources, 40 in unsheltered microhabitats and 40 in sheltered microhabitats. We recorded both the number of caches and seed consumption for each source. We found that plant cover affected the foraging activity of rodents of the sand dunes in the Monte Desert because both consumption and numbers of caches constructed from sheltered seed sources were higher than those from unsheltered ones. Consumption of sunflower was higher in the wet season than it was in the dry season, when millet consumption increased. Sunflower was the preferred seed both from sheltered or unsheltered sources. We discuss the possible causes of the different foraging strategies used by rodents of the Monte Desert.

**Key words:** Desert rodents, foraging strategies, seed removal, South American deserts.

### INTRODUCTION

Deserts are characterized by low rainfall, marked temperature contrasts, and by the temporal and spatial unpredictability of food resources (Costa 1995). In desert areas the sparse plant cover generates open areas where predation risk is high. Hughes and Ward (1993), Hughes *et al.* (1994) and Vásquez 1994) consider that predation risk strongly influences animal behaviour, and therefore that it is an important factor in modulating the pattern of animal activity (Kramer & Birney 2001), group size (McNamara & Houston 1992), foraging behaviour and microhabitat use (Hughes *et al.* 1994).

Several behavioural strategies are used by foragers in response to predators. Small mammals forage closer to cover, because sheltered microhabitats help them avoid predation (Parmenter & MacMahon 1983; Kotler *et al.* 1991, 1994a; Hughes & Ward 1993). Animals can use indirect environmental cues of predation hazard such as moonlight (Kotler *et al.* 1991, 1994a; Vásquez 1994). They can also carry food to sheltered sites in order to shorten the time of exposure in risky microhabitats (Vander Wall 1990; Hughes & Ward 1993; Vásquez 1994). Animals can select the size of food items they consume according to predation hazard, that is, they eat small items quickly in unsheltered sites, and

carry the bigger ones to protective cover for consumption (Lima 1985).

Given their usually sparse vegetation, deserts are appropriate environments to assess foraging decisions under predation risk, such as where, when, what and how much to eat (Brown 1988; Randall 1993; Hughes *et al.* 1994). The foraging strategies of the small mammals of South American deserts are still poorly known, except for those species occurring in the Chilean matorral (Vásquez 1994). Recently, Giannoni *et al.* (2001) found that small mammals hoard seed under shrubs, and that most caches are in sheltered microhabitats. These observations indicate that predation risk (Hughes & Ward 1993; Brown *et al.* 1994b; Kotler *et al.* 1994b), seed theft by birds and other rodents (Vander Wall 1990), or a favourable microclimate (Goodfriend *et al.* 1991) constitute foraging costs which are as important in the Monte Desert as in other desert areas of the world (Hughes & Ward 1993; Vásquez 1994). In the Monte Desert, potential predators of rodents that operate at sheltered sites include some snakes (Colubridae and Viperidae) in the wet season. In open areas, predatory birds (order Falconiformes: Accipitridae and Falconidae; order Strigiformes: Tytonidae and Strigidae; Ojeda *et al.* 1986), and carnivorous mammals (Canidae, Mustelidae and Felidae) operate all year round.

We were interested in assessing the effect of plant cover on the rate of seed removal by rodents of the Monte Desert for several reasons. First, comparative

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studies of the biology of small desert mammals are needed to ascertain the extent to which patterns described in one desert are also present in other deserts. Second, 70% of Argentina is desert and the Monte is one of the largest desert areas in the country. Furthermore, information on the Monte Desert could help us to understand processes that occur in other desert areas. Because one of the highest costs during foraging is the risk of predation, we expected rodents of the Monte Desert to use plant cover when foraging as a behavioural strategy to decrease predation risk in the same way that rodents do in other deserts where predation risk is very important in modulating their foraging activity (Kotler 1984; Brown 1988; Longland & Price 1991; Hughes & Ward 1993; Brown *et al.* 1994b; Kotler *et al.* 1994b).

In this study, we used artificial feeding stations to investigate the foraging strategies, seed collection, transport and consumption used by rodents of the Monte Desert in response to distance from seed sources to sheltered sites (i.e. shrubs) during two different seasons (wet and dry). We predicted that the two most abundant rodent species in the sand dunes (*Eligmodontia typus* and *Graomys griseoflavus*, Giannoni *et al.* 2001) would remove more seeds from protected seed sources because the risk of predation would be lower under than outside shrub canopies. Experiments on food preference for *G. griseoflavus* and *E. typus*, carried out under laboratory conditions, showed that millet was preferred to sunflower seeds, and that millet handling time was significantly shorter compared with sunflower (Tort *et al.* 1998). In the field, rodents must modulate their foraging activity in order to minimize the risk of predation, so we predicted that at sheltered sites, consumption of millet would be mostly based on preference. At unsheltered sites, individuals would trade off between seed handling time and predation risk, so we expected the smaller millet to be the most highly consumed seed at the source, and the larger sunflower seed to be transported under cover. We also predicted that in the dry season, when snakes are absent and the highest risk is in open areas where aerial and terrestrial predators (i.e. birds and mammals) are present, rodents would harvest more seeds from protected sources. In the wet season, when all predators are present, rodents would remove a similar quantity of seeds from sheltered and unsheltered microhabitats.

## METHODS

### Study area

Experiments on seed removal were carried out in the sand dunes of the Ñacuñán Reserve (Mendoza, Argentina). This reserve is located in the central area

of the Monte Desert (34°1'S, 67°58'W), which is one of the largest dry areas in Argentina. The Monte Desert consists mainly of an extensive shrubland dominated by *Larrea* spp. interspersed with open woodlands of *Prosopis* spp. (Morello 1985). The Ñacuñán Reserve comprises a diverse mosaic of habitats and plant communities, including mesquite forests (*Prosopis flexuosa*) and creosotebush communities (*Larrea divaricata* and *L. cuneifolia*). Sand dunes (Medanal) are characterized by sandy soils with a herbaceous stratum composed of *Panicum urvilleanum*, *Solanum euacanthum* and *Hyalis argentea*, and a shrub stratum including mainly *Larrea divaricata*, *L. cuneifolia* and *Condalia microphylla* (Roig 1981).

### Pilot study

In order to know the sources from which seeds were transported, we dyed the seeds with two colours used in confectionery: orange was used for sheltered sources and green for unsheltered sources. According to Carroni and Giannoni (2000) there was no significant preference by rodents for either colour. In a pilot trial, we placed 10 seed sources at open sites and 10 sources at protected sites.

### Main experiment

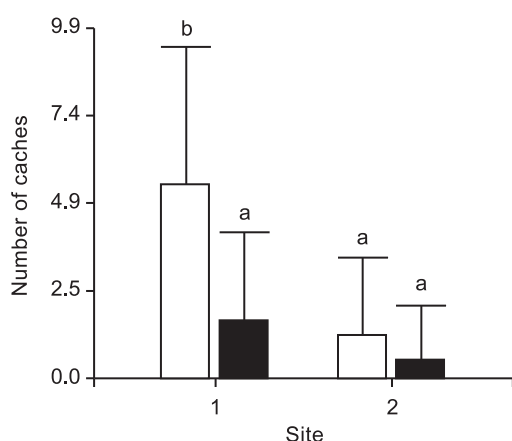
We evaluated the relative rates of seed removal by rodents in February and June 1999 (wet and dry season, respectively), at two sites 4 km apart. At each site we placed 40 seed trays (seed sources) 10 m apart along a 400-m transect across a sand dune of homogeneous vegetation and topography. Seed trays were alternated from one in an unsheltered microhabitat (2 m from the nearest shrub), to one in a sheltered microhabitat (directly under a shrub). We also placed eight control seed trays (four in unsheltered and four in sheltered microhabitats) on each site in order to estimate the changes in seed weight produced by external environmental conditions.

Trays consisted of plastic dishes (15 cm in diameter and 3 cm deep) filled with commercial seeds: 50 g sunflower mixed with 50 g millet. We used these two species of seeds because a previous study conducted in the field at the same site revealed that most caches contained sunflower seeds (Giannoni *et al.* 2001), whereas tests in laboratory conditions showed that rodents preferred millet (Tort *et al.* 1998). Trays were protected from seed removal by birds with a wire screen (40 cm × 40 cm × 7 cm), with two openings of 5 cm on each of the four sides that allowed only rodents to enter, and without openings in control trays to exclude rodents. Access by ants was prevented by placing the dishes above the ground surface.

For 48 h rodents were allowed access to artificial seed sources. Trays were not visited during the experiments to reduce disturbance of the foraging behaviour of rodents. At the end of the 2-day trial all remaining seeds were collected and weighed. The amount of seed removed per dish was obtained by subtraction from the initial supply.

We assumed, as have other authors, that seeds missing from each source were taken by small mammals (rodents), that consumers were able to handle at least one type of the seeds offered; and that interactions among rodent species were similar to those occurring at a natural seed source (Parmenter *et al.* 1984; López de Casenave *et al.* 1998; Sassi 2001). At the end of the trial we recorded all caches found in an area of 16 m<sup>2</sup> around each seed tray. These caches were assigned to the nearest source based on pilot trials, on the evidence of rodent tracks, and on the fact that the largest previously recorded distance of seed transported by rodents was 580 cm (Giannoni *et al.* 2001).

We considered a clump of shells and whole seeds to be caches, but never regarded single seeds as such, because they might have been occasionally dropped by an individual while foraging (Giannoni *et al.* 2001).



**Fig. 1.** Mean number of caches (mean  $\pm$  SD) for both experimental and replicate sites (site 1 and site 2). Letters (a,b) indicate differences between means (Tukey test,  $P < 0.0001$ ).  $F(1,154) = 6.07$ ;  $P < 0.0149$ . (□), sheltered; (■), unsheltered.

Seed caches were partially exposed, and only partially covered with sand and dry leaves, and therefore were easy to find (Giannoni *et al.* 2001). We also recorded the type of seed (millet or sunflower) that was found in the caches, mean cover of shrubs with caches underneath, and the degree of shelter provided by shrubs. To quantify shelter we recorded mean shrub height, considering only those branches less than 60 cm from the ground because Giannoni *et al.* (2001) found that shrubs with higher branches do not constitute a sheltered microhabitat for rodents of this community.

Analyses of variance (ANOVA) were used to test the effect of distance from seed sources to plant cover, as well as the influence of seed type and season on the foraging activity. Activity was estimated from the number of caches and seed consumption (results were expressed as mean  $\pm$  SD.). Data on seed consumption were transformed to meet ANOVA assumptions of normal distribution and homogeneity of variances using  $\log(x + 1)$  (Underwood 1997). Tukey tests were carried out to assess differences between treatments. Spearman correlations were also used.

## RESULTS

### Pilot study

Results showed that of a total of 60 caches discovered, 42 contained orange seeds from sheltered sources, and these 42 caches were all nearer sheltered than unsheltered sources (binomial test,  $P < 0.001$ ). Of the 18 caches that contained green seeds from unsheltered sources, only one was found near a sheltered source, whereas 17 were nearer unsheltered sources (binomial test,  $P < 0.001$ ).

### Main experiment

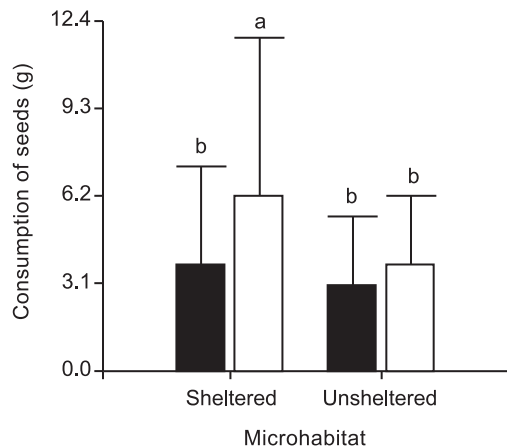
Plant cover significantly affected the foraging activity of rodents because there were more caches from sheltered seed sources (275) than from unsheltered

**Table 1.** Summary of analysis of variance for number of caches for two treatments (unsheltered and sheltered microhabitats), during two seasons (dry and wet) at two sites

Source of variation	d.f.	MS	F	P
Source	1	30.1	30.9	0.0000
Site	1	59.7	61.2	0.0000
Season	1	9.2	9.4	0.0025
Source/Sites	1	5.9	6.1	0.0149
Source/Season	1	1.4	1.4	0.2359
Site/Season	1	8.1	8.3	0.0045
Source/Site/Season	1	0.2	0.2	0.6651

ones (86) (Table 1, Fig. 1). Interactions between treatment and season were not significant. All caches were composed of sunflower, none of them contained millet, the smaller seed.

Seed consumption (Fig. 2) was significantly affected by all factors: treatment (sheltered and unsheltered sources), site, season and seed type. Interactions among these factors were significant and had a similar effect on both seed consumption and number of caches. Interaction between treatment and season were not significant. Interactions between treatment and seed type were significant. Consumption from sheltered sources was significantly higher for sunflower than for millet, whereas consumption from unsheltered sources was similar for both species of seeds (Table 2, Fig. 2). Plant cover had a significant effect not only on the number of caches but on seed consumption as



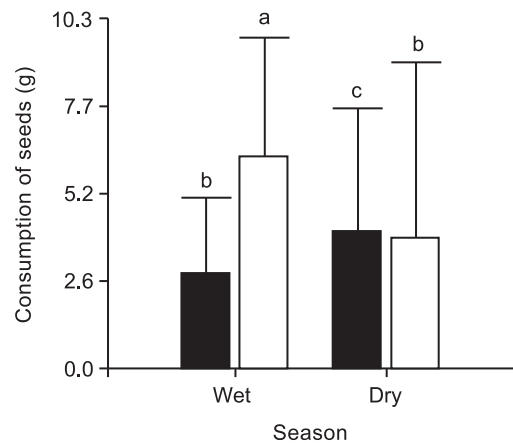
**Fig. 2.** Consumption of (□) sunflower and (■) millet seeds (mean  $\pm$  SD) in sheltered and unsheltered microhabitats. Letters (a, b) indicated differences between means (Tukey test,  $P < 0.0001$ ).  $F(1.306) = 4.73$ ;  $P < 0.0304$ .

well. Seed consumption was higher at sheltered than unsheltered seed sources (mean =  $10 \pm 8.6$  g, and  $6.8 \pm 4.1$  g, respectively).

Interactions between season and seed type were significant (Fig. 3). In the wet season, consumption of sunflower was significantly higher compared with millet, and millet was the most highly consumed seed in the dry season. Interactions among treatment, season and seed type were not significant (Table 2).

## DISCUSSION

Animals in the field have to modulate their foraging activity in response to several factors: food availability (Kotler 1984; Price & Waser 1985), cues of predation risk (Kotler 1984; Brown *et al.* 1994a; Brown *et al.*



**Fig. 3.** Consumption of (□) sunflower and (■) millet seeds (mean  $\pm$  SD) during a wet and a dry season. Letters (a,b,c) indicate differences between means (Tukey test,  $P < 0.0001$ ).  $F(1.306) = 70.02$ ;  $P < 0.000$ .

**Table 2.** Results of analysis of variance for seed consumption for two treatments (unsheltered and sheltered microhabitats), for two species of seed (millet and sunflower) during two seasons (dry and wet) at two sites

Source of variation	d.f.	MS	F	P
Source	1	0.66	7.91	0.0052
Site	1	6.92	83.33	0.0000
Season	1	1.81	21.79	0.0000
Seed	1	1.27	15.33	0.0001
Source/Site	1	0.44	5.29	0.0220
Source/Season	1	0.09	1.13	0.2876
Source/Seed	1	0.39	4.73	0.0304
Site/Season	1	1.93	23.22	0.0000
Season/Seed	1	5.82	70.01	0.0000
Site/Seed	1	0.04	0.48	0.4879
Source/Site/Season	1	0.02	0.30	0.5838
Source/Season/Seed	1	0.02	0.24	0.6254
Source/Site/Seed	1	0.03	0.31	0.5761
Season/Site/Seed	1	0.63	7.64	0.0060
Source/Site/Season/Seed	1	0.37	4.47	0.0352
Error	306	0.08		

1994b; Kotler *et al.* 1994b), harvest rate (Jenkins *et al.* 1995) and nutritional attributes (Lockard & Lockard 1971; Frank 1988). Hughes and Ward (1993) in the Namib desert, and Brown *et al.* (1994a) in the Negev desert found that rodents display higher foraging activity close to cover. Brown *et al.* (1994a) suggested that, under shrubs, rodents would find not only protection against predators but also a more favourable microclimate (Goodfriend *et al.* 1991). For Monte Desert rodents, predation could be a strong selective force very likely to affect their foraging decisions. Rodents prefer to forage close to cover where predation risk would be lower than at open sites away from shrubs where aerial and terrestrial predators are most likely to be present. Our results from long-term captures (1997–2002) have shown that the activity of Monte Desert rodents is not exclusively nocturnal (López de Casenave *et al.* 1998), as 40% of captures were during the daytime, and their activity changes seasonally (S. M. Giannoni, 1997–2002; S. Tabeni, 2000, pers. comm.). In the wet season, rodents removed a similar quantity of seeds from protected and unprotected sources. This would be mostly explained by the presence of snakes in sheltered microhabitats (Brown *et al.* 1994b; Kotler *et al.* 1994b) and of aerial predators in unsheltered microhabitats (Brown *et al.* 1994b). In the dry season, rodents harvested a similar quantity of seeds from both sources. From July to August, predation by the raptor *Athene cunicularia* is more frequent on rodents (Ojeda *et al.* 1986), so predation risk in open areas would be as important as the search for available food.

In risky areas, the forager must trade off energy gain against the risk of predation in deciding where and what to feed on (Lima & Dill 1990). Food handling time is an important cost because it can modify the size of items consumed. The black-capped chickadees (*Sciurus carolinensis*) change their foraging strategy depending on predation risk, eating small, easy-to-handle items at unsheltered sites, and transporting bigger items, requiring longer handling times, to safe sites under cover (Lima 1985). In unsheltered sources, we expected rodents to consume more millet directly from the source and sunflower to be carried under shrubs, assuming that decisions concerning where and what to eat depended on the handling time–predation risk trade-off. On the other hand, based on preference experiments (Tort *et al.* 1998; A. Orofino, unpubl. data), in sheltered sources we expected rodents to consume more millet than sunflower. Sand dune rodents in unsheltered sources seem to eat smaller seeds and transport larger ones. In the laboratory, the mean handling time (husking and chewing) was shorter for millet than for sunflower in both rodent species (*Eligmodontia typus*, millet =  $3.0 \pm 1.29$  s and sunflower =  $46.23 \pm 16.21$  s; *Graomys griseoflavus*, millet =  $4.33 \pm 2.32$  s and sunflower =  $17.34 \pm 5.52$  s;

Tort *et al.* 1998). At unsheltered sites, *E. typus* and *G. griseoflavus* could use a foraging strategy similar to that of the black-capped chickadee. However, at sheltered sources other factors seem to be involved, as sunflower was preferred over millet. Some studies suggest that under field conditions rodents become increasingly selective about which seeds they gather when foraging under high risk of predation (Hay & Fuller 1981; Bowers 1988). Terrestrial predation may be just as important as aerial predation. Perhaps both predation and microclimatic conditions, in relation to the thermal physiology of rodents (Caraco *et al.* 1990), are significant elements in determining the foraging success of animals.

Another important cost affecting foraging activity is travel cost. Because sand dune rodents have no pouches they must transport seeds one at a time, grabbing them with their incisors, so large seeds would provide them with a higher energy intake per travel unit (sunflower = 2343.88 J per 100 g *vs* millet = 1368.66 J per 100 g). Both in sheltered and unsheltered sources, rodents of the sand dunes consumed mainly sunflower seeds. A similar preference for larger seeds was reported by Lima and Valone (1986) for grey squirrels, and by Vander Wall (1995) for the yellow pine chipmunk. Preference for millet over sunflower was reported for desert-dwelling rodents in laboratory conditions (Frank 1988). However, in the field animals still have to contend with conspecifics, other competitors, and predators. Thus, animals cannot just eat only the food they prefer most, but must select food items based on abundance and any other beneficial attributes they may have. The sunflower seed is large, high in lipids, and low in carbohydrates and preformed water, whereas millet is the opposite (Price 1983; Tort *et al.* 1998). Seed handling time, seed size and energy content could be important attributes for Monte Desert rodents in the field in trading off the costs and benefits under predation pressure. This could affect decisions concerning where and what to eat.

In the sand dunes, V. Corbalan (pers. comm., 1999), based on captures, found the maximum relative abundance of adult and juvenile rodents to occur in autumn (April), a great number of pregnant females in spring (November), and a lower relative abundance in summer (February), when females had swollen nipples indicating that they were suckling (S. M. Giannoni, pers. obs., 2000, 2001). The fact that in the present study higher foraging activity was recorded in summer could reflect the demand by females within the population for energy, rather than an increased population abundance, because sunflower has a higher energy content than millet (Price 1983).

The two species considered in this study are omnivorous (Campos *et al.* 2001) rather than strictly granivorous, feeding on seeds, fruits, leaves and bark (M. Dacar & S. M. Giannoni, unpubl. data). Orofino

and Giannoni (2000), in preference experiments using natural seeds and fruits, found that *Eligmodontia typus* preferred mainly *Larrea divaricata* seeds followed by *Lycium chilense*; and *Graomys griseoflavus* preferred mainly *Lycium chilense* fruits. Thus, their generalist diet and the variable availability of different food items could allow rodents, in periods of food shortage, to modify the proportion of items consumed without having to change their foraging strategies by exposing themselves on risky sites far from protected cover. Perhaps the ability to store food is another reason why these species did not show changes in their foraging strategies in the dry season. Both *E. typus* and *G. griseoflavus* store food by scatter hoarding in the field (Giannoni *et al.* 2001), and by larder hoarding within their burrow systems both in the laboratory and under semicaptive conditions (Carroni & Giannoni 2000). This issue deserves in-depth research in the future.

In summary, plant cover affected the foraging activity of rodents of the sand dunes in the Monte Desert, because they foraged under cover in less risky microhabitats. Seed handling time and energy intake would be important attributes to be considered during the decision-making process regarding where and what to forage in situations of predation risk. The generalist diet of sand dune rodents could explain them not changing their foraging strategies under predation pressure (open areas) in periods of food shortage.

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## REFERENCES

- Bowers M. A. (1988) Seed removal experiments on desert rodents: The microhabitat by moonlight effect. *J. Mamm.* **69**, 201–4.
- Brown J. S. (1988) Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* **22**, 37–47.
- Brown J. S., Kotler B. P. & Mitchell W. A. (1994a) Foraging theory, patch use, and the structure of a Negev desert granivore community. *Ecology* **75**, 2286–300.
- Brown J. S., Kotler B. P. & Valone T. J. (1994b) Foraging under predation: A comparison of energetic and predation costs in rodent communities of the Negev and Sonora deserts. *Aust. J. Zool.* **42**, 435–48.
- Campos C. M., Ojeda R., Monge S. & Dacar M. (2001) Utilization of food resources by small and medium-sized mammals in the Monte Desert biome, Argentina. *Austral Ecol.* **26**, 142–9.
- Caraco T., Blanckenhorn W. U., Gregory G. M., Newman J. A., Recer G. R. & Zwicker S. M. (1990) Risk-sensitivity: Ambient temperature affects foraging choice. *Anim. Behav.* **39**, 338–45.
- Carroni I. & Giannoni S. M. (2000) Almacenamiento de alimento por *Eligmodontia typus* and *Graomys griseoflavus* (Muridae, Rodentia) en condiciones de cautividad y semicautividad. *XV Jornadas Argentinas de Mastozoología*. La Plata, Buenos Aires, Argentina.
- Costa G. (1995) *Behavioural Adaptations of Desert Animals*. Springer-Verlag, Berlin.
- Frank C. L. (1988) Diet selection by a heteromyid rodent: Role of net metabolic water production. *Ecology* **69**, 1943–51.
- Giannoni S. M., Dacar M., Taraborelli P. & Borghi C. E. (2001) Seed hoarding by rodents of the Monte Desert, Argentina. *Austral Ecol.* **26**, 259–63.
- Goodfriend W., Ward D. & Subach A. (1991) Standard operative temperatures of two desert rodent, *Gerbillus allenbyi* and *G. pyramidum*: The effects of morphology, microhabitat, and environmental factors. *J. Thermal Biol.* **16**, 157–66.
- Hay M. E. & Fuller P. J. (1981) Seed scape from heteromyid rodents: The importance of microhabitat and seed preference. *Ecology* **62**, 1395–9.
- Hughes J. J. & Ward D. (1993) Predation risk and distance to cover affect foraging behaviour in Namib desert gerbils. *Anim. Behav.* **46**, 1243–5.
- Hughes J. J., Ward D. & Perrin M. R. (1994) Predation risk and competition affect habitat selection and activity of Namib desert gerbils. *Ecology* **75**, 1397–405.
- Jenkins S. H., Rothstein A. & Green W. C. H. (1995) Food hoarding by merriam's kangaroo rats: A test of alternative hypotheses. *Ecology* **76**, 2470–81.
- Kotler B. P. (1984) Harvesting rates and predatory risk in desert rodents: A comparison of two communities on different continents. *J. Mamm.* **65**, 91–6.
- Kotler B. P., Ayal Y. & Subach A. (1994a) Effects of predatory risk and resource renewal on the timing of foraging activity in a gerbil community. *Oecologia* **100**, 391–6.
- Kotler B. P., Brown J. S. & Hasson O. (1991) Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* **72**, 2249–60.
- Kotler B. P., Brown J. S. & Michell W. A. (1994b) The role of predation in shaping the behaviour, morphology and community organisation of desert rodents. *Aust. J. Zool.* **42**, 449–66.
- Kramer K. M. & Birney E. C. (2001) Effect of light intensity on activity patterns of patagonian leaf-eared mice, *Phyllotis xanthopygus*. *J. Mamm.* **82**, 535–44.
- Lima S. L. (1985) Maximizing feeding efficiency and minimizing time exposed to predators: A trade-off in the black-capped chickadee. *Oecologia* **66**, 60–7.
- Lima S. L. & Dill L. M. (1990) Behavioral decisions made under the risk of predation: A review and prospectus. *Can. J. Zool.* **68**, 619–40.
- Lima S. L. & Valone T. J. (1986) Influence of predation risk on diet selection: A simple example in the grey squirrel. *Anim. Behav.* **34**, 536–44.
- Lockard R. B. & Lockard J. S. (1971) Seed preference and buried seed retrieval of *Dipodomys deserti*. *J. Mamm.* **52**, 219–21.
- Longland W. S. & Price M. V. (1991) Direct observations of owls and heteromyid rodents: Can predation risk explain microhabitat use? *Ecology* **72**, 2261–73.

- López de Casenave J., Cueto V. & Marone L. (1998) Granivory in the Monte Desert, Argentina: Is it less intense than in other arid zones of the world? *Global Ecol. Biog. Lett.* **7**, 197–204.
- McNamara J. M. & Houston A. I. (1992) Evolutionary stable levels of vigilance as a function of group size. *Anim. Behav.* **43**, 641–58.
- Morello J. A. (1985) *Grandes Ecosistemas de Sudamérica*. Proy. Prosp. Tecn. Amer. Lat, Text. Discusión FB/03, Fundación Bariloche, Buenos Aires, Argentina.
- Ojeda R. A., Pescetti E. & Monge S. (1986) *Ecología Trófica de Athene Cunicularia del Monte de Argentina*. X Congreso Latinoamericano de Zoología, Valparaíso, Chile.
- Orofino A. & Giannoni S. M. (2000) Preferencia de frutos y hojas de arbustos por *Eligmodontia typus* y *Graomys griseoflavus* en el desierto del Monte. *XV Jornadas Argentinas de Mastozoología*. La Plata, Buenos Aires, Argentina.
- Parmenter R. R. & MacMahon J. A. (1983) Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystems: The role of shrubs. *Oecologia* **59**, 145–56.
- Parmenter R. R., MacMahon J. A. & Vander Wall S. B. (1984) The measurement of granivory by desert rodents, birds and ants: A comparison of an energetics approach and a seed-dish technique. *J. Arid Environ.* **7**, 75–92.
- Price M. V. (1983) Laboratory studies of seed size and seed species selection by heteromyid rodents. *Oecologia* **60**, 259–63.
- Price M. V. & Waser N. M. (1985) Microhabitat use by heteromyid rodents: Effects of artificial seed patches. *Ecology* **66**, 211–19.
- Randall J. A. (1993) Behavioural adaptations of desert rodents (Heteromyidae). *Anim. Behav.* **45**, 263–87.
- Roig F. A. (1981) *Flora y vegetación de la Reserva Forestal de Ñacuñán*. Cuaderno Técnico 3–80. IADIZA Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza, Argentina.
- Sassi P. (2001) Heterogeneidad de la tasa de remoción de semillas por hormigas, aves y roedores a escala espacial y temporal en el desierto del Monte. Lic. Thesis, Universidad Nacional de San Luis, San Luis, Argentina.
- Tort J., Sarubbi R., Borghi C. & Giannoni S. M. (1998) Preferencia alimentaria y selección de semillas en cuatro especies de roedores del desierto: *Eligmodontia typus*, *Graomys griseoflavus*, *Calomys musculinus* y *Salinomys delicatus*. *XIII Jornadas Argentinas de Mastozoología*. Puerto Iguazú, Misiones, Argentina.
- Underwood A. J. (1997) *Experiments in Ecology. Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge University Press, Cambridge.
- Vander Wall S. B. (1990) *Food Hoarding in Animals*. University of Chicago Press, Chicago.
- Vander Wall S. B. (1995) Salivatory water loss during seed husking in deer mice and great basin pocket mice. *Physiol. Zool.* **68**, 878–86.
- Vásquez R. A. (1994) Assessment of predation risk via illumination level: Facultative central place foraging in the cricetid rodent *Phyllotis darwini*. *Behav. Ecol. Sociobiol.* **34**, 375–81.