

Hoarding patterns of sigmodontine rodent species in the Central Monte Desert (Argentina)

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Abstract Hoarding food is an important strategy of rodents in desert environments characterized by unpredictable and poor food resource availability. In the Monte Desert, *Prosopis* produces abundant food, unevenly in time and space, in the form of pods and seeds. Sigmodontine rodents (*Graomys griseoflavus*, *Akodon molinae*, *Eligmodontia typus* and *Calomys musculinus*) use *Prosopis* propagules extensively, and they could be predators or dispersers depending on how they handle and where they leave the propagules. The objectives of this study were: (1) to know what rodent species transported propagules; (2) to evaluate what hoarding pattern was used by species that transport propagules (larder and scatterhoarding); and (3) to analyse in which condition were propagules left by the rodent species, both at the food source and in caches. Our results showed that all four species transported propagules, with *G. griseoflavus* and *E. typus* being the species that carried more seeds. Our study supported the evidence that food caching is common among species and that many species both larderhoard and scatterhoard food. *Graomys griseoflavus* and *A. molinae*, the largest species, larderhoarded more than did the smaller *E. typus*. These results uphold the hypothesis that larger species will show greater propensity to larderhoard than smaller species. Considering the interaction between seed-hoarding patterns and plants, *E. typus* was the species that could most improve germination because it scatterhoarded propagules and left seeds out of pods. In contrast, *G. griseoflavus* could have a negative impact on plant populations because this was the species that predated more seeds and larderhoarded a high percentage of them. The smallest *C. musculinus* was the species that transported propagules least, and left them as seeds inside pods or pod segments mainly at the food source, which makes seeds more vulnerable to predation.

Key words: disperser, larderhoarding, predator, *Prosopis flexuosa*, scatterhoarding.

INTRODUCTION

Arid environments are heterogeneous ecosystems, characterized by unpredictable food resource availability and limited moisture availability for animals (Costa 1995). In these regions, some trees and scrubs, like *Prosopis* species, are key components (Mares *et al.* 1977) that produce abundant food, unevenly in time and space, in the form of pods and seeds (Fagg & Stewart 1994; Villagra *et al.* 2004). In deserts, rodents are the most diverse and abundant mammal group (Costa 1995), and the majority of them are omnivores (Kerley & Whitford 1994). *Prosopis* propagules are used by rodents who can play roles as predators or

dispersers (Reynolds & Glendening 1949; Reynolds 1950, 1954; Duval *et al.* 2005). In the Central Monte Desert, some small rodent species remove fruits (Campos *et al.* 2006), consume mesquite pods and seeds (Campos *et al.* 2001; Giannoni *et al.* 2005) and store food in caches (Campos *et al.* 2006). When the resource is temporally superabundant, the rodents store food in caches for future periods when propagules are scarce. This behaviour converts intermittent food sources into more reliable ones and enables individuals to have control over food supplies (Vander Wall 1990; Herrera & Pellmyr 2002).

Two major forms of food hoarding can be identified in animals: larderhoarding, in which food is stored at usually one or a few large sites concentrated in a small part of the territory, inside the burrow or near a nest; and scatterhoarding, in which inconspicuous pits are

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dug, each with one or a few food items, scattered throughout the home range of an animal (Randall 1993; Jenkins *et al.* 1995; Jenkins & Breck 1998). But these are usually the end-points of a continuum of spatial patterns of food storage (Jenkins *et al.* 1995). Several factors in this gradient come into play such as costs of storage and retrieval, nutritional value of propagules, distance between seeds and burrow, body size of animals in relation to propagule size, defence of caches, risk of inter- and intra-specific pilferage, risk of predation, habitat structure and interactions among sympatric species, among others (Randall 1993; Gálvez *et al.* 2009). Several studies suggest that sympatric rodents differ in their hoarding behaviour and that differentiation in seed hoarding may help coexistence among these species by reducing trophic niche overlap (Jenkins *et al.* 1995; Jenkins & Breck 1998; Price *et al.* 2000; Murray *et al.* 2006).

Differences in seed-hoarding behaviour could be related to body size of the species involved. For example, larderhoarding makes food unavailable to other individuals if the larderhoarder can defend its burrow successfully (Jenkins & Breck 1998). Therefore, it is predicted that larger species will larderhoard more than smaller species because the former can prevent pilfering of their stored food by both large and small species (Jenkins & Breck 1998), whereas the scatterhoarding behaviour presumably is related to an inability of individuals to protect, defend and recover large concentrations of food (Stapanian & Smith 1978; Clarkson *et al.* 1986; Jenkins & Breck 1998).

Elucidating the differentiation in seed hoarding among sympatric rodents may also help understand the role of specific rodents in the dynamics of plant communities. The relative benefits of seed dispersal by these animals to plant recruitment are difficult to estimate, and they can play the role of an antagonistic seed predator or a conditional mutualistic seed disperser (Vander Wall 1990; Theimer 2005). Animals that cache seeds for later consumption become potential seed dispersers (Vander Wall 2002) because the transport of propagules may in itself reduce seed predation around the parent plant, where seeds are more vulnerable (Fenner & Thompson 2005). When propagules are handled and hoarded by animals, there is a chance that seeds are released from their impermeable coat (Howe & Smallwood 1982; Vander Wall 1990; Baskin & Baskin 1998; Li & Zhang 2003; Hollander & Vander Wall 2004), improving their germination (Longland *et al.* 2001). Particularly, scatterhoarding may enhance the reproductive success of plants because it moves seeds away from parent and sibling plants (McAuliffe 1990; Vander Wall 1994), increases seed germination rates (McAdoo *et al.* 1983), and reduces seed loss to other foragers that consume seeds without caching them or that hoard seeds in unfavourable conditions for germination (e.g. larderhoards; Longland *et al.* 2001). Some

studies have even shown seeds dying from desiccation or predation if they were not removed and buried by scatterhoarding animals (e.g. Roth & Vander Wall 2005). Seeds in scattered caches, which are not recovered for later consumption, may germinate and contribute to recruitment in plant populations (e.g. Price & Jenkins 1986; Vander Wall 1994). Nonetheless, some studies showed that several rodent species can slow or stop germination of cached seeds of particularly fast-germinating trees by pruning their radicle or sprout, or even by removing the entire embryo (Jansen *et al.* 2006; Xiao *et al.* 2009; Yang *et al.* 2011).

There is relatively little information on hoarding by small mammals in South American arid regions (see review Kelt 2011). Also, research on how the foraging activities of small mammals and other taxa such as birds and ants affect the structure and function of desert ecosystems would be helpful in understanding to what extent the hypotheses stated for rodent species from North American deserts can be applied to other deserts of the world. Considering that the structure of the relationship between consumer and prey is highly contextual, subtleties can only be uncovered by further study of this interaction (see review Kelt 2011). A first step in understanding the potential role of food hoarding in the community ecology of South American deserts is comparing the hoarding behaviour of sympatric rodent species.

Four small sigmodontine rodents occur in the Central Monte Desert there: *Graomys griseoflavus*, *Akodon molinae*, *Eligmodontia typus* and *Calomys musculinus* that differ in body size and diet. In a previous study carried out in the field we found that these rodent species removed, transported and hoarded pods and seeds of *Prosopis flexuosa* (Campos *et al.* 2007). In that study only above-ground caches could be recorded, and they contained a low proportion of removed seeds, with recovered seeds reaching nearly 17% of the total amount. Recent evidence indicates that these rodents have the ability to find buried seeds (Taraborelli *et al.* 2009), and that they remove seeds from the dung of cattle (S Velez & C Campos, pers. comm., 2007). This evidence indicates that seeds would be a precious resource for these rodent species. In this framework the objectives of this study, using laboratory experiments, were: (1) to know what rodent species transported propagules; (2) to evaluate what hoarding pattern was used by species that transport propagules (larder and scatterhoarding); and (3) to analyse in which condition were the propagules left by the rodent species, both at the food source and in caches.

METHODS

We collected rodents at the Reserve of Ñacuñán 200 km south-east of Mendoza (Argentina) from 6 May 2004 to 25 June 2004, so the animals were captured at a time when they

had already been exposed to one fruiting period of *Prosopis* plants. This reserve comprises approx. 13 000 ha of xerophytic vegetation corresponding to the Monte ecoregion of plains and plateaux (Monte de Llanuras y Mesetas; Burkart *et al.* 1999). The reserve is located in the central-western part of the Mendoza Plain (34°02'S, 67°58'W), 200 km south-east of Mendoza (Argentina). The climate is semiarid with a long-term average annual rainfall of 322 ± 103 mm (SD, range 192–533; $n = 17$ years), concentrated in the summer months (November–March; mean = 235.22 ± 89.5 mm). Mean monthly temperatures range from less than 10°C in winter to more than 20°C in summer (Ojeda *et al.* 1998). This reserve encompasses a diverse mosaic of habitats and plant communities including mesquite woodlands (*P. flexuosa* D.C.), creosotebush (*Larrea divaricata* Cav. and *L. cuneifolia* Cav.), saltbush (*Atriplex lampa* Gill. ex Moq.) and sand dune communities (Ojeda *et al.* 1998). All four rodent species used were collected from the sand dune community characterized by having vegetation patches with a herbaceous stratum composed of *Panicum urvilleanum* Kunth, *Solanum euacanthum* Phil. and *Hyalis argentea* Don ex H. et A., a shrub stratum including mainly *L. divaricata* and *L. cuneifolia*, and an arboreal stratum dominated by *P. flexuosa* (Roig 1971; Asner *et al.* 2003).

We studied four sigmodontine rodent species that varied in body size and diet. *Graomys griseoflavus* (Waterhouse 1873) is the largest sigmodontine (mean weight of 59.4 g; Giannoni *et al.* 2001); *A. molinae* (Contreras 1968) has a mean weight of 40 g; *E. typus* (F. Cuvier 1837) is a small rodent (mean weight of 21.4 g), and *C. musculus* (Thomas 1913) weighs approx. 17.5 g. None of these rodent species has cheek pouches or is strictly granivorous. However, seeds comprise between 20% and 60% of the diet of these small rodents (Campos *et al.* 2001; Giannoni *et al.* 2005).

All individuals used were adults: 12 *G. griseoflavus*; 14 *E. typus*; 11 *A. molinae* and 8 *C. musculus*. Before beginning the laboratory trials, animals were maintained for 2 months in individual metal or plastic home cages containing a layer of fine sand and a can for nesting to allow them to habituate to laboratory conditions. During this time rodents were provided food *ad lib* and fed on a diet of carrot, apple, oat and mixed seed (sunflower and millet). Animals were kept under a 14 h/10 h light–darkness cycle and temperature varied between 15°C and 21°C. All experiments were carried out under the same light cycle.

The experiment was conducted with propagules of *P. flexuosa* because they are consumed by all rodent species (Campos *et al.* 2001; Giannoni *et al.* 2005). The fruit is an indehiscent pod with a thin epicarp and a mesocarp that can be fleshy, sugary or fibrous. Every seed is protected inside an indehiscent woody endocarp and has an impermeable seed coat, physical barriers to hinder germination (Catalán & Balzarini 1992). Propagules of *P. flexuosa* are not chemically protected and are consumed by several species, including humans (Álvarez & Villagra 2009). The pod is on average 15.8 cm long (range 12–19), 0.78 cm wide (range 0.5–1.1) and weighs 4.6 g (range 2–9.6). Each pod contains 9–15 seeds (24–40 mg; Burkart 1976).

Trials were carried out in an arena similar to that used by Jenkins *et al.* (1995). The arena consisted of four wooden boxes (100 cm length \times 100 cm width \times 43 cm height) filled to a depth of 3 cm with fine sand for scatterhoarding seeds.

The bottoms of the boxes consisted of a piece of fine-mesh screening over a removable wooden board; when we removed the board to drain the sand from the boxes, seed caches remained in place on the screen for counting. All boxes were covered with hardware cloth to prevent escape of animals. The boxes were connected in a linear series by three polyvinyl chloride tubes, which represented 235-cm-long runways. One of the boxes was also connected to a small food-box that simulated a food source (20 cm length \times 20 cm width \times 16 cm height), in which we placed *P. flexuosa* propagules. In the box connected with the food-box we placed cotton as nesting material.

We began each trial by depositing an animal into the food-box late in the afternoon, placing the nesting material from its home cage in the food-box, and providing a known number of seeds (mean 156, range 151–173) inside fresh pods (between 10 and 12 pods). During the experiment, individuals were tested one at a time and the order of individuals was random among and within species. Before each trial, the boxes were carefully cleaned and sand was replaced in order to eliminate odour cues. After 48 h we removed the animal from the arena and returned it to its home cage. In all tests performed, for all species of rodents, we made sure that the seeds offered always exceeded the amount that could be consumed. Then we counted the number of seeds in the food-box and the number of seeds larderhoarded in the tubes, and drained the sand from the arena to count the number of seeds in all scatterhoards that had been buried in the sand. In no case did the runways (tubes) have sufficient sand to allow burying of the propagules. We considered those seeds consumed in the food-box to have been manipulated at the food source but not transported, seeds stored in tubes to be larderhoards, and seeds buried in the sand of the arena to be scatterhoards. To learn about the condition of seeds in caches after the experiments, we classified seeds as: (i) predated seeds (including endocarps with no seeds and coats with no seeds); (ii) seeds out of pods (i.e. seeds with endocarp); and (iii) seeds in pods or pod segments. We registered what rodent species had transported propagules from the food-box (i.e. food source), where these propagules were stored (larderhoards and scatterhoards), and in which condition the rodents species left them (at the food source and in both kinds of caches) after 48 h.

We used generalized models (GLM) and generalized linear mixed models (GLMM) in all analyses. Models were fitted with a Poisson distribution (and log-link function was used; McCullagh & Nelder 1989) because the data were counts. The significance of fixed factors was tested using the Wald statistical test. The sign of parameters having significant effects was used to interpret the results (McCulloch & Searle 2001; Bolker *et al.* 2008). In order to assess differences among species in the number of transported propagules (Objective 1), we fitted a GLM using rodent species (with four levels: *G. griseoflavus*, *C. musculus*, *A. molinae*, *E. typus*) as fixed effects, body size as covariate and number of transported seeds as the response variable. To compare among species the pattern for hoarding transported seeds (Objective 2), we fitted a GLMM considering rodent species and hoarding patterns (with two levels: larderhoarding and scatterhoarding) as fixed effects, body size as covariate, and number of seeds stored in larderhoards and scatterhoards as the response variable. Each individual was considered a random factor accounting for the

lack of independence of the observations at the site where rodents manipulated the seeds or pods. For analysing differences among species in the condition of seeds remaining at the food source and of those transported to caches (Objective 3) we fitted three GLMM with three response variables: number of predated seeds, seeds out of pods and seeds in pods. We considered two fixed effects: rodent species (with four levels) and site where they handled the seeds (larderhoards, scatterhoards and food source). For all models, the studied individual was considered a random factor, thus accounting for the lack of independence of the observations at the site where rodents manipulated the seeds or pods. In assessing the number of seeds stored by rodent species we could only compare, using a χ^2 -test, the size of scatterhoarded caches; because the tubes of the device intended to simulate runways are not made of transparent material, we were not able to record the size of larderhoarded caches. All statistical analyses were carried out using RStudio statistical software version 0.95.265 (Free Software Foundation, Inc., 2009–2011; <http://www.rstudio.org/>).

RESULTS

All rodent species transported propagules of *Prosopis*; however, the number of *Prosopis* seeds was different when compared among rodents species considering body size as covariable (Wald test = 50860.5; d.f. = 5; $P \leq 0.01$). Body size was significantly different among species, the heaviest being *G. griseoflavus*, followed by *A. molinae*, *E. typus* and *C. musculus* (Wald test = 59.8; d.f. = 1; $P \leq 0.001$). As a result, *G. griseoflavus* and *E. typus* were the species that transported more propagules (41% and 33% respectively; Wald test = 372; d.f. = 3; $P \leq 0.01$; Table 1), whereas *C. musculus* and *A. molinae* were the ones to leave more propagules at the source (91% and 79% respectively).

Also there were differences between hoarding patterns used by species, that is, larderhoarding or scatterhoarding, considering body size as a covariable (Wald test = 1188; d.f. = 12; $P \leq 0.01$; Table 1). All four rodent species showed different patterns for hoarding food (interaction rodent species-hoarding

behaviour: Wald test = 867.8; d.f. = 3; $P = 0.01$). At one extreme, the largest species *G. griseoflavus* and *A. molinae* were the species that larderhoarded more seeds (Wald test = 24136.7; d.f. = 5; $P = 0.01$), reaching 80% and 89% of the transported seed, respectively, and on the other extreme, the small species *E. typus* was the one that scatterhoarded more seeds in the sand-filled boxes in the arena (Wald test = 17524.5; d.f. = 5; $P = 0.01$), reaching 83% of the transported seeds (Table 1). *Calomys musculus*, the smallest species, cached few seeds either in scatterhoards or in larderhoards (Table 1). Considering the sizes of scatterhoarded caches, there were no differences among species in the number of seeds stored per cache ($\chi^2 = 3.6$; d.f. = 1; $P = 0.059$). However, a tendency was found, *E. typus* being the species that scatterhoarded more seeds per cache (mean \pm SE = 20.9 ± 4.7), followed by *C. musculus* (17.8 ± 11.3), *G. griseoflavus* (7.8 ± 2.1) and *A. molinae* (4.8 ± 2.4).

For comparing the condition of harvested seeds in relation to the site where propagules were left, that is, in caches (larderhoards and scatterhoards) or at the food source, results showed that rodent species differed in the number of predated seeds they left (Wald test = 72.1; d.f. = 3; $P \leq 0.001$), being significant also the interaction between rodent species and site (Wald test = 191.8; d.f. = 4; $P \leq 0.01$; Fig. 1). Compared with the other species, overall *G. griseoflavus* was the one to eat more seeds, although *E. typus* consumed more seeds in scatterhoards and at the food source (Fig. 1).

Rodents consumed the pods from a high percentage of propagules, leaving seeds with endocarp out of the pods. There was a significant effect of species (Wald test = 138.7; d.f. = 4; $P \leq 0.01$) and the rodent species-site interaction (Wald test = 472.1; d.f. = 6; $P \leq 0.01$). In general, *A. molinae* and *G. griseoflavus* were the species that left more seeds in this condition, but the small *E. typus* left the highest number of seeds with endocarp out of the pods in scatterhoards (Fig. 1).

Finally, all species left a high percentage of seeds contained in pod fragments at the source, especially

Table 1. Number of *Prosopis* seeds (percentage) transported (scatterhoarded and larderhoarded) and not transported by the rodent species *Graomys griseoflavus*, *Akodon molinae*, *Eligmodontia typus* and *Calomys musculus*

Rodent species	Total seeds (100%)	Number of seeds at source	Transported	
			Scatterhoarded	Larderhoarded
<i>G. griseoflavus</i>	2791	1658 (59%)	220 (8%)	913 (33%)
<i>A. molinae</i>	2148	1700 (79%)	48 (2%)	400 (19%)
<i>E. typus</i>	3207	2154 (67%)	878 (27%)	175 (6%)
<i>C. musculus</i>	1624	1474 (91%)	89 (5%)	61 (4%)

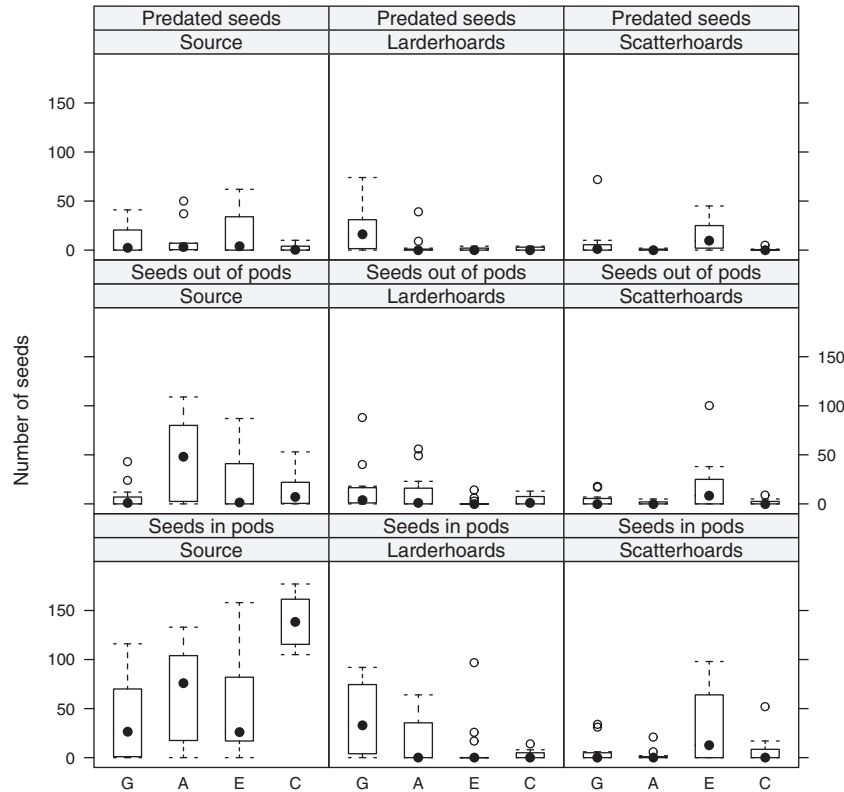


Fig. 1. Number of *Prosopis* seeds in different conditions (predated seeds, seeds out of pods and seeds in pods) that were left in larderhoards, scatterhoards and food source by the rodent species *Graomys griseoflavus* (G), *Akodon molinae* (A), *Eligmodontia typus* (E) and *Calomys musculus* (C).

C. musculus and *A. molinae* (Wald test = 1007; d.f. = 6; $P \leq 0.01$). Instead, *E. typus* and *G. griseoflavus* stored seeds in this condition in scatterhoards and larderhoards respectively (Fig. 1).

DISCUSSION

All species transported *Prosopis* propagules, particularly *G. griseoflavus* and *E. typus*. However *C. musculus* and *A. molinae* left almost all propagules at the food source, and a high percentage of these seeds were in pods or pod segments. The pod of *P. flexuosa* is a relatively large legume (approx. length = 15 cm; Capparelli 2008) so rodents might have to break the pods in order to transport them. All rodents studied could be imperfect harvesters that leave more than half the seeds contained in pods at the source. Imperfect harvesting is associated with situations where animals extensively harvest temporally superabundant seeds, and store excess food in caches for future use (Herrera & Pellmyr 2002). From the seed point of view, permanence at the source and contained in pod fragments could make seeds more vulnerable to predation, because fragments are easily harvested by other seed-eaters such as ants and birds.

Our observations support the evidence that caching is common among sigmodontine species and that

many of them make both larderhoards and scatterhoards as do other desert rodent species (Vander Wall 1990; Jenkins & Breck 1998; Price *et al.* 2000). *Graomys griseoflavus* and *E. typus* were the species that transported more propagules to larderhoard and scatterhoard. In the case of *G. griseoflavus*, the largest and dominant species in the mesquite woodlands of the Monte Desert (Corbalán & Ojeda 2004), transporting pods would be a strategy that could confer advantages when the food is an important source of nutrients and large in size, such as the propagules of *Prosopis* (Reynolds & Glendening 1949). Even though body size could affect the capacity to transport pods, with larger species being more capable for this task, also other factors seem to be involved in food transport by sigmodontine rodent species. For a small rodent such as *E. typus*, that occurs frequently in risky habitats with open vegetation (Ojeda 1989; Giannoni *et al.* 2001; Corbalán & Ojeda 2005), a behavioural strategy to minimize predation risk could be taking the food to a safe site and caching it, instead of handling it directly at the source, so as to shorten the time of exposure in risky microhabitats (Vander Wall 1990; Hughes & Ward 1993; Taraborelli *et al.* 2003). In contrast, *C. musculus* utilizes microsites with high grass cover (Ojeda & Tabeni 2009), and *A. molinae* prefers densely vegetated areas and undisturbed patches with high

plant cover (Corbalán & Ojeda 2004; Tabeni *et al.* 2007). In consequence, the low propensity showed by these species to transport propagules from the food source could be explained by their use of less risky microhabitats.

Regarding the second objective, our evidence supports the hypothesis that larger species will show a greater tendency to larderhoard than smaller species, a similar pattern to that found for heteromyid rodents by Jenkins and Breck (1998) and Price *et al.* (2000). *Graomys griseoflavus* is strong and aggressive (Redford & Eisenberg 1989; Giannoni *et al.* 2001) and the largest species studied, followed in body size by *A. molinae*. According to the hypothesis that larderhoarding is an adaptive behaviour for species that can defend concentrated food caches (Jenkins & Breck 1998), the large body size of *G. griseoflavus* and *A. molinae* could explain this hoarding pattern. On the other hand, *E. typus* and *C. musculus* are the smallest species and there is no evidence that they are aggressive (S Giannoni, pers. obs., 2001), so they could be less successful defending concentrated food caches. Also, the studied rodent species have a differential ability to find buried seeds, with *E. typus* being the most successful species, and *G. griseoflavus* the least successful (Taraborelli *et al.* 2009). Scatterhoarding involves a well-developed sense of smell that allows finding food caches (Vander Wall *et al.* 2005). The differential ability to find seeds found by Taraborelli *et al.* (2009) agrees with our results, indicating a greater propensity in *E. typus* to scatterhoard and in *G. griseoflavus* to larderhoard food. This implies that *E. typus* moves and scatters the *Prosopis* seeds, and could also relocate them more than do other species. Future studies could show the abilities of rodent species to find *Prosopis* seeds in similar conditions to those in caches.

Food storage could be an important strategy for rodent species because a rich resource becomes available in the season of scarcity or in less productive years (Smith & Reichman 1984; Vander Wall 1990; Jenkins *et al.* 1995). In fact, small rodents in the Monte Desert consume pods and seeds during the dry season (autumn and winter; Giannoni *et al.* 2005; Rosi *et al.* 2009), when propagules are not available because fruiting occurs in summer, and their persistence on the soil surface is very brief (Villagra *et al.* 2002) and non-existent in the soil bank (Marone *et al.* 1998). Thus, seed caching could offer the animals a solution for overcoming the overall shortage of food resources in harsh desert environments.

Seed-hoarding rodents, moreover, have effects on landscape dynamics, because they can play the role of an antagonistic seed predator or a mutualistic seed disperser (Vander Wall 1990, 1993; Theimer 2005). *Graomys griseoflavus* and *E. typus* were the most predatory species, but they were also the rodents that transported more seeds. This active dual role could depend

on different factors related to animal behaviour, such as the sites where seeds were hoarded, and the conditions in which propagules were left in caches.

In a previous study on removal of mesquite seeds by rodents in the Monte Desert it was found that they removed and scatterhoarded *Prosopis* pods and seeds (Campos *et al.* 2007). Rodents removed on average 30% of the seeds provided, 17% were recovered in detected scatterhoards, and the fate of the remaining removed seeds, 83% on average, was uncertain (Campos *et al.* 2007). This study found a low percentage of predated seeds (0–1.4%), 25% of seeds were out of the pods, and 51–61% of seeds were inside pods or pod segments. As our present study was carried out in laboratory conditions, we tried to understand the fate of seeds that we did not find during the field study. Based on our results, the low percentage of predation found in the field could be because *G. griseoflavus* is the species that consumed more seeds, but in larderhoards, and the experimental design used did not allow detection of these caches during the field study. Therefore, the presence of predated seeds and seeds outside pods in scatterhoards in the field study could be the result of pod handling by *E. typus*.

Because of the interaction between seed-hoarding rodents and plants, larderhoarded seeds are unlikely to germinate; so although the hoarding behaviour would be advantageous to rodents, it has a negative impact on plant populations (Price & Jenkins 1986). On the other hand, scatterhoarded seeds may germinate if they are not recovered by rodents, but impact on seeds will depend on the condition in which rodents leave the seeds in caches. All rodents could have some positive effect on the dispersal of *P. flexuosa* as they left some seeds out of pods in scatterhoards. *Eligmodontia typus* was the species that could most improve seed germination because it scatterhoarded 27% of the transported seeds, leaving 30% of them out of pods.

Regarding the harvested seeds left in larderhoards, there are at least two potential costs: conditions for germination are not suitable because *Prosopis* seeds need sites with high percentage of incident light (Páez & Marco 2000; Vilela & Ravetta 2000); and seeds stored in the relatively warm, moist environment of a burrow may be more likely to be attacked by microbes, fungi or insects (Reichman *et al.* 1986; Jenkins *et al.* 1995). Although *G. griseoflavus* transported an important number of propagules and some of them were cached in a condition to germinate (seeds out of pods and seeds in pods), they were left mainly in larderhoards. Also, *G. griseoflavus* was the species that killed more seeds at all sites, and then it would be the species most likely to have a negative effect on seed survival.

Food storage has strong implications to the community ecology of rodents, both in structure and in function, through redistribution of seeds via different hoarding patterns (Daly *et al.* 1992; Jenkins & Breck

1998; Price *et al.* 2000). Caching plays a critical role in competition, both exploitative and interference, among heteromyid rodent species and between rodents and other seed-eaters (Brown & Heske 1990; Jenkins *et al.* 1995). In the Monte Desert, the role of caching in community organization is perhaps less important because small rodents are not strongly granivorous and also use other resources such as leaves, stems and arthropods (Campos 1997; Campos *et al.* 2001; Giannoni *et al.* 2005). However, further studies will be necessary in order to know the role of transport and storage of seeds by small rodents in the structure and functioning of the community in the Monte Desert.

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