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Removal of mesquite seeds by small rodents in the Monte desert, Argentina

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Abstract

We examined the removal of *Prosopis flexuosa* pods by small rodents, and addressed four specific questions: (1) do Monte Desert small rodents remove mesquite pods? (2) if they do, do they store them above-ground? (3) how far are pods carried? and (4) what condition are removed pods and seeds in? We carried out the experiments in March 2000 and June 2003, at two sand-dune sites in the Ñacuñán Reserve, Mendoza plain (Argentina), where *Eligmodontia typus*, *Graomys griseoflavus*, *Akodon molinae*, and *Calomys musculinus* (Sigmodontidae) are present. On each site we established 32 feeding stations. We recorded the weight of pods and the number of seeds left on the dishes, number of seeds and weight of pods removed, number of caches and their distances from trays, and the condition of pods and seeds in the caches. We found that rodents did remove and scatterhoard *Prosopis* pods; in many cases rodents only removed the exocarp and mesocarp. Over a 48-h period rodents removed 42% and 18% of the seeds provided in 2000 and 2003, respectively. In 2000, we only recovered 13% of the removed seeds in the 58 caches detected; in 2003, we found 20.4% of the removed seeds in the 55 caches detected. The fates of remaining removed seeds (87–79.6%) is uncertain. Pods in caches exhibited a different degree of damage caused by rodents: seeds outside pods amounted to 25%, endocarps with no seeds represented only 0–1.4%, and 51–61% of the seeds were inside pods or pod segments.

Keywords: *Prosopis flexuosa*; Mammals; Pods; South American arid lands

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1. Introduction

The effect of animal activities on both fruits and seeds is an interesting aspect of seed ecology, that includes plant–animal interactions such as dispersal, predation, storing, and stimulating germination (Baskin and Baskin, 1998). The benefits of these interactions (e.g. scarification of surviving seeds, planting of seeds, relocating cached seeds at better germination sites, rapid removal from the vicinity of the parent plant, etc.), can be high for the seeds that survive handling by animals (Chambers and MacMahon, 1994; Traveset and Verdú, 2002; Li and Zhang, 2003).

In seeds of desert trees (as the genus *Prosopis*), germination is often hindered by physical dormancy (Burkart, 1952), associated with water-impermeable seed coats (Barton, 1965). Under natural conditions, seed dormancy could be broken by animals, fire, and soil abrasion (e.g. Lamprey et al., 1974; Sabitti and Wein, 1987; Gutterman, 1994). Consumption and manipulation of pods and seeds by animals are also likely to affect dormancy breaking, viability, and germination in seeds.

During pod consumption by large and medium herbivores, seeds accidentally enter the digestive system of animals and they can be defecated in conditions suitable for germination. Numerous studies show the significant role that wild and domestic animals play in the dispersal and germination of Fabaceae seeds through pod consumption (Eilberg, 1973; Peinetti et al., 1992, 1993; Cox et al., 1993; Campos and Ojeda, 1997; Pratolongo et al., 2003).

The feeding activities of small animals on fruits and seeds do not always imply seed ingestion, and may result in holes being cut in the impermeable seed coat; thus, seeds may be mechanically scarified, as well as dispersed away from the parent plant, although some seeds are killed in this plant–animal interaction (Baskin and Baskin, 1998; Hollander and Vander Wall, 2004), as occurs in seed interaction with medium and large mammals (Campos and Ojeda, 1997). For example, food-hoarding animals, by storing, burying, and manipulating seeds, influence the germination process and seedling regeneration as well (Howe and Smallwood, 1982; Vander Wall, 1990; Li and Zhang, 2003).

In arid and semi-arid areas of Argentina, the effect of small mammals on pods and seeds by removal, consumption, and dispersal remains unknown. Sigmodontine rodents of the central Monte Desert consume pods and seeds of mesquite (*Prosopis flexuosa* D.C.; Campos et al., 2001; Giannoni et al., 2005), and experiments on removal performed with commercial seeds have shown that some species (*Eligmodontia typus* and *Graomys griseoflavus*) store harvested seeds in shallow depressions in the soil and in leaf litter (Giannoni et al., 2001; Taraborelli et al., 2003b).

Within this framework, we examined the removal of mesquite pods by small rodents, and addressed four specific questions: (1) do Monte Desert small rodents remove mesquite pods? (2) if they do, do they store them above-ground? (3) how far are pods carried? and (4) what condition are removed pods and seeds in?

2. Materials and methods

2.1. Study area

The experiment was carried out at the Reserve of Ñacuñán, located in the central-western part of the Mendoza Plain (34°02′S, 67°58′W), 200 km south-east of Mendoza, Argentina. The Reserve is in the Monte phytogeographic province (Morello, 1958) and comprises approximately 13 000 ha of xerophytic vegetation. The climate is semi-arid with a long-term average annual rainfall of 322 ± 103 mm (SD, range 192–533; $n = 17$ yr), concentrated in the summer months (November–March; mean $= 235.22 \pm 89.5$ mm) (Campos, 1997). Mean daily temperatures are lower than 10 °C in winter and above 20 °C in summer.

This reserve comprises a diverse mosaic of habitats and plant communities including mesquite forests (*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; Asner et al., 2003). The study was conducted at two sites within the sand-dune community, which is characterized by sandy soils with a herbaceous stratum composed of *Panicum urvilleanum* Kunth, *Solanum euacanthum* Phil., and *Hyalis argentea* Don ex H. et A., among others (Roig, 1971; Asner et al., 2003).

2.2. Small mammals

Four sigmodontine species occur in the sand dunes studied: the silky mouse (*E. typus* F. Cuvier, 1837), the gray leaf-eared mouse [*G. griseoflavus* (Waterhouse, 1873)], the grass mouse (*Akodon molinae* Contreras, 1968), and the vesper mouse [*Calomys musculinus* (Thomas, 1913)]. *E. typus* is a small rodent (mean weight = 21.4 g) that occurs in sandy and warm habitats (Ojeda, 1989; Redford and Eisenberg, 1989). This species is in many respects comparable to the heteromyid rodents of North America: *E. typus* occurring at open sites exhibits a greater tendency to jump during escapes and uses an erratic escape behavior as found for the kangaroo rat *Dipodomys merriami* (Taraborelli et al., 2003a), probably forages in and around bushes and bounds rapidly across open areas, stores food, and can exist for long periods with no free water (Mares, 1973; Ojeda, 1989; Redford and Eisenberg, 1989). *G. griseoflavus* is the largest sigmodontine (mean weight = 59.4 g), and resembles a small *Neotoma*; it is found in areas that are typically xeric but include cultivated fields, semi-arid sandy areas with rocks, hillsides with boulders, and orchards (Redford and Eisenberg, 1989). *A. molinae* (mean weight = 32 g) uses habitats with high cover of shrubs, herbs and litter (Redford and Eisenberg, 1989; Corbalán, 2004). *C. musculinus* weighs approximately 17.5 g (Redford and Eisenberg, 1989).

The relative abundance of each small rodent in sand-dune habitats of Ñacuñán in 2002 was calculated as the number of animals captured per 100 trap-nights for live traps. In one area, *G. griseoflavus* represented 25 animals/100 trap-night, *A. molinae* 27.5, *C. musculinus* 3.75, and *E. Typus* 11.25. In the other area, *G. griseoflavus* represented 36.25 animals/100 trap-night, *A. molinae* 1.25, *C. musculinus* 10, and *E. typus* 6.25 (Giannoni, unpublished data).

With respect to diets, *E. typus* and *A. molinae* are omnivorous, although the latter exhibits a strong tendency to insectivory, *C. musculinus* is granivorous, and *G. griseoflavus* herbivorous (Campos et al., 2001; Giannoni et al., 2005). Rodent species display considerable trophic flexibility that may be particularly advantageous in arid environments where resource availability is unpredictable and heterogeneous.

From the data obtained in the mesquite community of Ñacuñán, *E. typus* is the species showing higher consumption of fruits (32.5%), whereas *G. griseoflavus* consumes 5.5%, *A. molinae* 4% of fruits, and *C. musculinus* less than 1% (Campos et al., 2001). In sand dunes, the study allow to differentiate fruits and seeds in diets. *E. typus* includes 13% of *Prosopis* pods, and 0.17% of *Prosopis* seeds, whereas the diet of *G. griseoflavus* is composed of 10.7% of pods, and 0.06% of seeds. *A. molinae* and *C. musculinus* eat less than 5% of pods and seeds (Giannoni et al., 2005).

2.3. Removal experiments

The mesquite fruit is an indehiscent pod, with a relatively soft exocarp (Burkart, 1976). The mesocarp is thick and contains the major portion of sugars and starches (Kingsolver et al., 1977) as well as proteins. Seeds are covered with an endocarp and a seed coat. The endocarp is bony and acts as a barrier that inhibits germination (Warrag, 1994), and as a physical defense against herbivores.

We carried out the experiments at the beginning of the dry season (March 2000 and June 2003), at two sand-dune sites (Sites 1 and 2) in the Ñacuñán Reserve. During those months no natural pods are available in the environment selected, therefore animals could only use the pods we supplied. On each site we established 32 feeding stations, 10 m apart. One tray was placed in each station, accessible only to rodents. Trays consisted of plastic dishes (inaccessible to ants because of their depth and smooth texture that prevented ants from climbing), 15 cm in diameter and 3 cm deep, containing known fresh weights of mesquite pods (mean = 21.6 g) with their seeds inside (number of *Prosopis* seeds: mean = 249, range: 229–262). Trays were protected from pod removal by birds with a wire screen (40 cm × 40 cm × 7 cm) with two 5-cm openings that allowed only small rodents to enter. Dishes were placed in the evening, at the edge of perennial shrubs (because at the Monte desert plant cover affects seed removal by rodents; Taraborelli et al., 2003b), and remained in the field for 48 h.

At the end of the 2-day trial, we recorded the weight of pods and the number of seeds left on the dishes, number of seeds in the caches, distance of caches from trays, and the condition of pods and seeds in the caches. We considered a clump of pod segments, whole pods and seeds to be caches, but never regarded single seeds or pods as such, for they might have been occasionally dropped by a subject during transport. We were able to find the caches because they were partially exposed, partly covered with sand and dry leaves. Pod removal was estimated as the difference between the initial weight of the pod supply and the weight of the pods that remained on the dishes at the end of the experiment.

2.4. Observational data

Complementarily to our experiment, in March 2002, along three 50-m long transects, we sampled the caches under 12 fruiting mesquite trees that showed rodent activity. We described the condition of seeds and pods in caches as indicated below.

2.5. Condition of pods and seeds in caches

To learn about the effect on pods and seeds of transport and manipulation by animals, and to answer in part the fourth question addressed, we described the condition of seeds in the caches after experiments. Seeds were classified as: (1) seeds outside the pods, with endocarp; (2) predated seeds—endocarp with no seeds; and (3) seeds in pods or pod segments.

For caches found in the field, outside our experiment, we considered the following as predated seeds: only endocarps with no seeds; only coat with no seeds; only endocarps, no seeds in whole pods or pod pieces; spaces without seeds in whole pods or pod pieces.

3. Results

We found that rodents did remove and scatterhoard mesquite pods and seeds, in many cases removing the endocarps. In each feeding station ($N = 128$), over the experiment, the mean weight of offered pods was 21.56 g (SE = 0.08). The mean weight of pods removed per feeding station was 6.70/48 h (SE = 0.66), representing 30% of the weight of pods supplied. Pod removal ranged from 0.0 to 22.9 g/48 h (Site 1: mean = 3.55, SE = 0.72; Site 2: mean = 9.84, SE = 0.98 both years).

In 2000, mean weight of pods removed was 9.19 (SE = 0.96). The total seed supply on both study sites was approximately 15 900; rodents removed about 6650 seeds (42% of the seeds provided). We only recovered 13.26% of the removed seeds (882 seeds) in the 58 caches detected. In 2003, mean weight of pods removed was 4.28 (SE = 0.83) in both sites. The total seed supply in this year on both study sites was approximately 6678; rodents removed about 1213 seeds (18% of the seeds provided). We found 20.4% of the removed seeds (247 seeds) in the 55 caches detected. We failed to establish the fate of the remaining removed seeds (79.6% and 86.7%) in both years.

The mean number of caches detected by feeding station was 0.9 (SE = 0.18). In 2000, the mean was 0.90 (SE = 0.16; $N = 58$) and in 2003, 0.86 (SE = 0.33; $N = 55$).

At Site 1, the mean distance between caches and pod sources was 24.24 cm (SE = 4.66, maximum = 85, minimum = 1.15), and at Site 2 it was 64.32 cm (SE = 5.21, maximum = 200, minimum = 1.81).

In the caches we found that seeds outside pods amounted to 20–24%, endocarps with no seeds represented only 0–1.4%, and the remaining seeds were inside pods or segments of pods (Table 1).

With respect to caches observed in the field, we found that seeds outside pods amounted to 3.25%. These caches showed more signs of seed predation (only endocarps with no seeds; only coat with no seeds; only endocarps, no seeds in whole pods or pod pieces; spaces without seeds in whole pods or pod pieces) than caches found in removal experiments, which indicated that 50.35% of the seeds had been preyed upon (Table 1).

4. Discussion

Rodents inhabiting the Monte desert removed and transported mesquite pods, although caches found above-ground contained only a low proportion of the seeds removed (13% in 2000 and 18% in 2003). We do not know the fate of the rest of the mesquite pods supplied. However, preliminary results of experiments made in captivity found that rodent species store seeds and pods above-ground (scatter hoarding) and also inside burrows (larder hoarding) (Giannoni and Campos, unpublished data). Anecdotal field data also suggest that rodents in the field store seeds inside burrows (Natalia Borruel, personal communication), as they do in captivity, which would account for the high percentage of seed removed that we were unable to find.

Seed-hoarding rodents can act as predators and dispersers of plants (Vander Wall, 1993). Seed loss is the cost for the plant, but caching may increase seedling establishment

Table 1
Condition of seeds in caches in 2000 ($N = 58$), in 2003 ($N = 55$), and in caches observed in the field in 2002 ($N = 53$) (we considered the following as predated seeds: only endocarps with no seeds; only coat with no seeds; only endocarps, no seeds in whole pods or pod pieces; spaces without seeds in whole pods or pod pieces)

Condition of seeds	Total[a]	%	Maximum[b]	Mean[c]	SD
Experimental data					
2000					
Seeds outside pods, with endocarps	174	19.7	31	3.05	6.70
Predated seeds—only endocarp	12	1.4	6	0.21	0.88
Seeds in pods and pod segments	696	78.9	80	12.21	13.00
Total seeds in caches ($N = 58$)	882	100			
2003					
Seeds outside pods, with endocarps	59	23.9	14	0.95	1.83
Predated seeds—only endocarp	0				
Seeds in pods and pod segments	188	76.1	17	3.03	4.79
Total seeds in caches ($N = 55$)	247	100			
Caches observed in the field (2002)					
Seeds outside pods					
Without endocarps	4	0.2	4	0.01	0.20
With endocarps	70	3.1	14	0.18	1.04
Seeds in pods and pod segments	1055	46.4	16	2.72	3.53
Predated seeds	1145	50.3	39	2.95	4.21
Total seeds in caches ($N = 53$)	2274	100			

[a] Total number of seeds in all caches.
[b] Maximum value of seed number per cache.
[c] Mean value per cache.

(Forget, 1993; Longland et al., 2001). On the one hand, transport of propagules may in itself reduce seed predation around the parent plant, as in this place seeds will be more vulnerable than widely scattered individuals (Fenner and Thompson, 2005). Moreover, the most suitable sites for the establishment and growth of *Prosopis* seedlings are arid microsites far from tree canopies, with high percentages of incidence of light (Páez and Marco, 2000; Vilela and Ravetta, 2000). On the other hand, the result of imperfect harvesting is that a certain proportion of seeds accidentally escape destruction, thus converting genuine harvesters into occasional seed-dispersers. Seed dispersal based on imperfect harvesting is associated with situations where animals intensively harvest temporally superabundant seeds, and store the excess food in caches for future use (Herrera and Pellmyr, 2002).

Another hypothesis that can explain the low number of seed recovered could be cache predation by other mammal species such as *Ctenomys* sp., *Dolichotis patagonum*, *Lepus europaeus,*and *Microcavia australis,* that abound at the study site (Ojeda et al., 1998). Pilferage by conspecifics and other species is a frequent event, as was suggested by Jenkins et al. (1995).

Pods were transported 200 cm from the source at most. However, a much longer experiment (Giannoni et al., 2001) reports that rodents in the same area of the Monte desert transport commercial seeds as far as 580 cm. The dispersal distance recorded in this study is short compared to that found by Giannoni et al. (2001) probably because pods are much larger and heavier than commercial seeds. Even though pods are transported only a short distance away from the source, dispersal by rodents may be beneficial to plants because it complements other dispersal mechanisms (Chambers and MacMahon, 1994).

Caches included whole pods, pod segments, seeds with endocarp, and single endocarps. Therefore, after rodent activity, many seeds are outside the pod and do not remain concentrated under the trees, on account of which seeds are less exposed to be preyed upon when pods are attacked by predators (e.g. insect larvae; Janzen, 1969, 1980; Aizen, 1991).

The ways in which food hoarders handle the items they store influence their effectiveness as agents of plant dispersal (Vander Wall, 1990). Experiments conducted in the laboratory (Orofino, 2006) and observational data of this study, show that some rodent species are capable of opening the endocarp and eating the seeds. Observational data reveal that caches contain 50% of the seeds with evidence of rodent predation. However, the results of field experiments indicate that rodents only remove the exocarp and mesocarp; whereas neither the endocarp nor the seed coat, both closely associated with dormancy and germination inhibition (Barton, 1965; Warrag, 1994), seem to be very affected (0–1.4%). These differing results may be due to the short time that the animals were in contact with the caches during the field experiments. The removal of the exocarp and mesocarp of mesquite seeds could be the beginning of the complex process of dormancy breaking, that leaves the seeds exposed to the action of other factors, such as soil abrasion.

The role of Monte rodents in dispersing mesquite pods and seeds seems to be similar to that of rodents in other arid and semi-arid lands (Reynolds and Glendening, 1949; Mares et al., 1977). In sum, small rodents remove mesquite pods, build food caches above-ground, and partly remove the exocarp and mesocarp of pods. They have no important harmful effects on most seeds in the caches, which maintain their endocarp undamaged, leaving the seeds exposed to the action of other factors, such as soil abrasion. Given the hardness of the mesquite endocarp, rodents probably need more handling time to open it and remove the seeds, which would enhance their risk of predation. We suppose that rodents also store pods and seeds inside burrows, as they do in captivity experiments; and for this reason we did not find 87–80% of the mesquite pods supplied. Therefore, these burrow-stored seeds are likely to suffer higher damage because animals will handle them for a longer time, as they also constitute a food reserve.

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