Role of small rodents in the seed dispersal process: *Microcavia australis* consuming *Prosopis flexuosa* fruits

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Abstract Understanding the functional role of animal species in seed dispersal is central to determining how biotic interactions could be affected by anthropogenic drivers. In the Monte Desert, mammals play different functional roles in *Prosopis flexuosa* seed dispersal, acting as opportunistic frugivores (endozoochorous medium-sized and large mammals) or seed hoarders (some small sigmodontine rodents). Our objective was assessing the functional role of *Microcavia australis*, a small hystricognathi rodent, in the fruit removal and seed deposition stages of *P. flexuosa* seed dispersal, compared to sympatric sigmodontine rodents. *In situ*, we quantified fruit removal by small rodents during non-fruiting and fruiting periods, and determined the distance seeds were transported, particularly by *M. australis*. In laboratory experiments, we analysed how *M. australis* stores seeds (through scatter- or larder-hoarding) and how many seeds are left in caches as living seeds, relative to previous data on sigmodontine rodents. To conduct field studies, we established sampling stations under randomly chosen *P. flexuosa* trees at the Ñacuñán Man and Biosphere Reserve. We analysed fruit removal by small rodents and seed dispersal distance by *M. australis* using camera traps focused on *P. flexuosa* fruits covered with wire screen, which only allowed entry of small animals. In laboratory trials, we provided animals with a known number of fruits and assessed seed conditions after removal. Small rodents removed 75.7% of fruit supplied during the non-fruiting period and 53.2% during the fruiting period. *Microcavia australis* and *Graomys griseoflavus* were the main fruit removers. *Microcavia australis* transported seeds to a mean distance of 462 cm and cached seeds mainly in scatter-hoards, similarly as *Eligmodontia typus*. All transported seeds were left in fruit segments or covered only by the endocarp, never as predated seeds. *Microcavia australis* disperses *P. flexuosa* seeds by carrying fruits away from a source to consume them and then by scatter-hoarding fruits and seeds.

Key words: larder-hoarding, rodent, scatter-hoarding, seed dispersal, seed predation.

INTRODUCTION

Seed dispersal is a critical step in a plant's life cycle, with important consequences for seedling establishment, population genetics, demography, spatial distribution, conservation and evolution (Traveset & Rodríguez-Pérez 2008). Seed dispersal by animals involves reciprocal benefits, with nutritional rewards for animal species and dispersal services for plants (Vander Wall & Beck 2012). Animals that ingest fruits and defecate or regurgitate seeds (frugivores) and animals that store seeds (hoarders) can inadvertently disperse some seeds, contributing to the natural plant regeneration cycle (Vander Wall & Beck 2012).

There are two major types of seed hoarding behaviour identified in animals: larder-hoarding, in which food is stored in underground burrow chambers at usually one or a few large sites concentrated in a small part of the territory, and scatter-hoarding, when animals store seeds in well-spaced caches in the ground (Jenkins & Breck 1998; Vander Wall & Beck 2012). Considering that in larder-hoarding, seeds are stored in a dark, warm and moist environment of a burrow, where germination conditions are unfavourable and seeds are more likely to be attacked by microbes, fungi or insects (Longland *et al.* 2001; Vander Wall & Beck 2012), only those animals that scatter-hoard seeds in the soil surface, returning later to eat many but not all of them, could be considered effective dispersers of seeds (Price & Jenkins 1986; Vander Wall 2002; Vander Wall & Beck 2012). Therefore, scatter-hoarding may enhance the reproductive success of plants because seeds are moved away from parent and sibling plants (McAuliffe 1990; Vander Wall 1994), and seed loss to other

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seed predators (e.g. insects, birds) and pilferers is reduced (Vander Wall 1993; Forget *et al.* 1994). When fruits are handled and hoarded by animals, the seed can be freed from fruit structures that delay germination; also, feeding activities may result in holes bored into the impermeable seed coat (Howe & Smallwood 1982; Vander Wall 1990; Baskin & Baskin 1998; Li & Zhang 2003; Hollander & Vander Wall 2004) allowing water entry and improving seed germination rates (McAdoo *et al.* 1983; Longland *et al.* 2001). Scatter-hoarding animals include some species of rodents (e.g. tree squirrels, chipmunks, mice, kangaroo rats, spiny rats, some caviomorph rodents), corvids (e.g. jays, rooks, nutcrackers) and marsupials (Vander Wall & Beck 2012).

In drylands across the world, *Prosopis* fruits and seeds are an attractive food for wild and domestic animals (Kingsolver *et al.* 1977; Campos *et al.* 2008). For example, the fruit of *Prosopis flexuosa* is an indehiscent legume with a thin exocarp, a thick mesocarp that contains the major proportion of sugar and starches, and several hard endocarp segments protecting the seeds (Kingsolver *et al.* 1977). This fruit is an important dietary contribution for animals as a good hydrocarbonated food with relatively low fibre and discrete quantities of protein and fat (Wainstein & González 1971). The seeds show a high protein content and have impermeable seed coats that cause physical dormancy and inhibit germination (Catalán & Balzarini 1992; Warrag 1994). Only a few days after reaching the soil, *P. flexuosa* fruits are removed by mammals, among other animals. On the one hand, some opportunistic frugivores disperse seeds by endozoochory (dispersal following fruit consumption and passage through the digestive tract of an animal), such as medium-sized native mammals (e.g. *Dolichotis patagonum*, *Lagostomus maximus*, *Lycalopex griseus*), large native herbivores (e.g. *Lama guanicoe*) and non-native animals (e.g. *Lepus europaeus*, *Sus scrofa*, *Equus asinus*; Campos & Ojeda 1997; Villagra *et al.* 2002; Campos *et al.* 2008, 2011). On the other hand, small sigmodontine rodents (up to 100 g; e.g. *Graomys griseoflavus*, *Akodon molinae*, *Eligmodontia typus*, and *Calomys musculinus*) behave as food-hoarding animals and they make both larder-hoards and scatter-hoards (Campos *et al.* 2007; Giannoni *et al.* 2013).

The small hystricognathi rodent *Microcavia australis* (up to 400 g) also consumes *P. flexuosa* fruits (Campos 1997; Sassi *et al.* 2011). This species is a diurnal and semi-fossorial social rodent that lives in gallery burrow systems built in association with *P. flexuosa* trees (Tognelli *et al.* 1995, 2001). As mentioned before, there is information about the functional role of sigmodontine rodents, some of the species being mainly predators that larder-hoard seeds, and others being dispersers of *P. flexuosa* seeds through their scatter-hoarding behaviour (Campos *et al.* 2007; Giannoni *et al.* 2013), but how the co-occurring small hystricognathi rodent *M. australis* acts in the seed dispersal process is still unknown. Understanding the functional role of animal species in the seed dispersal process is central to determining how biotic interactions considered indicators of ecosystems' 'health' are affected by anthropogenic drivers (Valiente-Banuet *et al.* 2014).

In this framework and considering that fruit removal and food caching depend in part on seasonal patterns of fruit availability and increase in anticipation of a decline in resource availability (e.g. the dry season; Jansen & Forget 2001), our objective was to evaluate the functional role of *M. australis* in the fruit removal stage of dispersal and in the seed deposition stage in comparison with sympatric sigmodontine rodents. For this, in field studies, we quantified fruit removal by *M. australis* and other small rodents during both non-fruiting and fruiting periods, and we analysed the distance seeds were transported particularly by *M. australis*. Moreover, in a laboratory experiment, we analysed how seeds are stored by *M. australis* (through scatter-hoarding or larder-hoarding) and, if there is scatter-hoarding, how many seeds are left in caches as living seeds (seeds inside endocarps and sometimes also covered by another fruit part), relative to previously obtained data on sigmodontine rodents (Giannoni *et al.* 2013).

METHODS

Field study

The study was conducted in the Man and Biosphere Reserve of Ñacuñán (34°02′S; 67°58′W, 540 m a.s.l.; Mendoza Province). This site belongs to the temperate Monte Desert biome, and it shows marked seasonality with humid summers (mean temperature >20°C) and dry winters (mean temperature < 10°C). Average annual rainfall is 324 mm concentrated in the summer months. The area boasts a diverse mosaic of habitats that includes *P. flexuosa* woodland, *Larrea cuneifolia* shrubland and sand dunes (Roig 1971). *Prosopis flexuosa* is considered a key species at the ecosystem level because it plays a fundamental role in ecosystem structure and functioning, mainly in plant–animal interactions (Mares *et al.* 1977).

To quantify fruit removal by *M. australis* and the other species of small rodents, we carried out an experiment during the non-fruiting period (May–June 2014), when only a few fruits still remain on the ground because their persistence on the soil surface is very brief (Villagra *et al.* 2002), and during the fruiting period (February–March 2015). We established 30 sampling stations randomly chosen in *P. flexuosa* woodland (15 for each period). Each sampling station was located under a *P. flexuosa* tree (all with similar crown volume), with a minimum distance between them of 500 m. This design allowed us to consider each station as

an independent sample because the home range of the studied species does not exceed 300 linear m (Corbalán & Ojeda 2005). At each sampling station, 20 *P. flexuosa* fruits (containing 15 seeds each) were offered during 48 h. Fruits were covered with a wire screen (40 cm length × 40 cm width × 7 cm height) with two 5-cm × 5-cm openings, following Campos *et al.* (2007). This system allows the entry of small mammals and prevents birds and bigger mammals from accessing the fruits. The short fruit exposure time helped avoid fruit removal by ants (Campos C., pers. obs.). In order to identify animal species and quantify the number of fruits removed by each of them, we placed a camera trap (Moultrie 990i) at 1.80 m height focused on each sampling station. The cameras took pictures whenever animal movement was detected, with a 30-s delay between consecutive pictures. The location of the cameras allowed us not only to identify species but also to count the number of remaining fruits and seeds after the mammal left the feeding station (Grünewald *et al.* 2010).

To determine how far seeds were transported, we established sampling stations under 10 *P. flexuosa* trees. Under each tree, to ensure the removal of fruit by *M. australis,* we placed 10 coloured *P. flexuosa* fruits (100 seeds in total) during the daylight hours of 1 day, covered with the wire screen and with cameras taking pictures as described above. Fruits were marked using water-soluble paint. At the end of the day, removed fruits were searched for within a 20-m radius, and we recorded the number of seeds in the caches and the distance of caches from the fruit source.

Laboratory study

To analyse the functional role of *M. australis* in the seed deposition stage, we captured 10 adult *M. australis* individuals at the Man and Biosphere Reserve of Ñacuñán using Havahart live traps (20 × 20 × 50 cm; Woodstream Corporation, Lititz, PA, USA) and Tomahawk live traps (14 × 14 × 40 cm; TomahawkLive TrapCo., Tomahawk, WI, USA). Before beginning the laboratory trials, animals were maintained for 2 months in 1 × 1 × 2 m individual metal home cages situated in an outdoor place with a layer of fine soil to allow them to habituate to captivity conditions. During this time, animals were provided with food and water *ad libitum* and fed on a diet consisting of alfalfa, apple and *P. flexuosa* fruits. Animals were kept under a natural light–darkness cycle and all experiments were carried out under the same light cycle.

Trials were conducted in the same arena used by Giannoni *et al.* (2013) for further comparison with sigmodontine rodents. It consisted of four wooden boxes (100 cm length × 100 cm width × 43 cm height) filled to a depth of 3 cm with fine sand. Boxes were connected in a linear series by three PVC 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 × 20 cm width × 16 cm height), inside which we placed *P. flexuosa* fruits. The bottoms of the boxes consisted of a piece of fine-mesh screen over a removable wooden board; when we removed the board to drain the sand from the boxes, seed caches stayed in place on the screen for counting.

We began each trial by depositing an animal into the food-box late in the afternoon and providing a known number of seeds (mean = 156, range = 151–173) inside fresh fruits (between 10 and 12 fruits). In all tests performed, seeds offered always exceeded the amount that could be consumed. During the experiment, individuals were tested one at a time and the order of individuals was random. After 48 h, we removed the animal from the arena and returned it to its home cage. Then, we counted the number of seeds in the food-box and in the tubes, and drained the sand from the arena to count the number of seeds. We considered those seeds stored in tubes to be larder-hoards, and seeds buried in the sand of the arena to be scatter-hoards. To assess the condition of stored seeds after the experiments, we classified seeds as: (1) predated seeds (endocarps with no seeds and coats with no seeds) and (2) living seeds (seeds inside endocarps and sometimes also covered by another fruit part).

Statistical analysis

To assess whether fruit removal in the field differed among *M. australis* and other small rodents during non-fruiting and fruiting periods, we fitted a generalised linear model (GLM) with a Poisson distribution (McCullagh & Nelder 1989) because the response variable was the number of fruits removed. We specified the species of rodent removing fruits as a fixed factor.

To assess the functional role of *M. australis* in seed deposition using laboratory results, we fitted a GLM considering the place where seeds were stored (with two levels: larder-hoarding and scatter-hoarding) as a fixed factor. As the response variable was a proportion (number of seeds in larder- or scatter-hoards/number of supplied seeds minus number of seeds in larder- or scatter-hoards), we assumed a binomial error structure and used a logit link function (McCullagh & Nelder 1989). Regarding scatter-hoarding of living seeds, in order to compare the results from this study with results from the previous study on hoarding patterns of sigmodontine rodents (*G. griseoflavus*, *A. molinae*, *E. typus,* and *C. musculinus*; for details see Giannoni *et al.* 2013), we built a GLM considering species as a fixed factor and the proportion of seeds left in scatter-hoards (number of living seeds left in scatter-hoards/number of supplied seeds − number of living seeds in scatter-hoards) as the response variable. Because the fitted model exhibited overdispersion ($\hat{c} = 35.95$), we adjusted a binomial negative distribution (Burnham & Anderson 2002).

In all cases, the significance of fixed factors was tested using the Wald statistical test (McCulloch & Searle 2001). All statistical analyses were carried out using R Core Team (2014). We used the package 'aod' for Wald Statistical test (Lesnoff & Lancelot 2012).

RESULTS

In the field, small rodent species removed 75.7% of fruit supplied during the non-fruiting period, and 53.2% of fruit supplied in the fruiting period. During

Table 1. Percentage of fruits removed (mean ± SE) by small rodent species during non-fruiting and fruiting periods

Species	Percentage of fruits removed	
	Non-fruiting period	Fruiting period
Microcavia australis	12.67 (±7.50) a	21.07 (±7.85) a
Galea musteloides	–	1.78 (±1.78) b
Ctenomys mendocinus	–	0.71 (±0.71) b
Graomys griseoflavus	63.00 (±10.87) b	26.78 (±5.59) a
Akodon molinae	–	2.86 (±1.87) b

Different letters show significant differences among species for each period ($P < 0.05$; Wald test).

the non-fruiting season, *G. griseoflavus* and *M. australis* were the only species caught by camera traps. Results showed that *G. griseoflavus* removed significantly more *P. flexuosa* fruits than *M. australis* (Wald test; $\chi^2 = 1246.1$, $P < 0.01$; Table 1). During the fruiting season, the small hystricognathi rodents *M. australis*, *Galea musteloides* and *Ctenomys mendocinus*, and the sigmodontine rodents *G. griseoflavus* and *A. molinae* removed fruits. *Microcavia australis* and *G. griseoflavus* were the species that removed the highest proportion of fruits (Wald test; $\chi^2 = 348.8$, $P < 0.01$; Table 1). After offering 100 fruits (containing 1000 seeds in total) only to *M. australis*, it removed 90% of fruits supplied and we were able to find 26.5% of the seeds contained in these fruits. Seeds were located in partially exposed caches of 2–20 seeds, partly covered with sand and dry leaves. The mean distance between caches and offered fruits was 462 cm (SE = 57.35, maximum = 1400, minimum = 10).

In the laboratory, *M. australis* cached seeds in both scatter-hoards (mean % ± SE = 52.8 ± 9.3) and larder-hoards (22.7 ± 8.4), but significantly more seeds were stored in scatter-hoards (Wald test; $\chi^2 = 646.2$, $P < 0.0001$). All seeds transported by *M. australis* were left in fruit segments or covered only by the endocarp, and never were predated seeds found in caches.

When comparing the number of living seeds in scatter-hoards left by *M. australis* in the laboratory experiment with data previously obtained for sigmodontine rodents, we found that there was no significant difference between this species and *E. typus*, whereas *M. australis* left more living seeds in scatter-hoards than did *G. griseoflavus*, *A. molinae* or *C. musculinus* (Table 2).

DISCUSSION

Like sigmodontine rodents, the small hystricognath rodent *M. australis* removed, transported and hoarded fruits and seeds of *P. flexuosa*. Our results showed that *M. australis* stores fruits and seeds mainly in scatter-hoards, consuming fruits but not seeds of *P. flexuosa*. Food caching is a common strategy for rodent species that could buffer food shortage during harsh weather conditions or in less productive years (Vander Wall 1990; Jansen & Forget 2001). Particularly, scatter-hoarding occurs in a reduced diversity of terrestrial vertebrates across the world (Vander Wall & Beck 2012), including small rodents (e.g. spiny mice, squirrels, chipmunks, mice, kangaroo rats; Vander Wall 1990; Yasuda *et al.* 2000; Theimer 2001; Midgley & Anderson 2005) and marsupials (e.g. musky rat-kangaroo; Forget & Vander Wall 2001; Dennis 2003).

When we compared *P. flexuosa* fruit removal by different small rodents, *G. griseoflavus* and *M. australis* were the major removers. During the non-fruiting period, these were the only rodent species to remove *P. flexuosa* fruits, particularly *G. griseoflavus*. *Graomys griseoflavus* is the dominant sigmodontine rodent in the mesquite woodland of the Monte ecoregion and increases in abundance during the non-fruiting period (April–May) due to recruitment of juveniles born in the summer months (Corbalán & Ojeda 2004). Thus, during the non-fruiting period, considering the high abundance of *G. griseoflavus* and its intensive fruit removal activities, the persistence of fruits fallen under the trees represents a disadvantage to the plant because these fruits are

Table 2. Percentage (mean ± SE) of living *Prosopis flexuosa* seeds left in scatter-hoards by small rodents during the laboratory study

Species	Percentage (SE) of living seeds in scatter-hoards	Chi-square (Wald test)	d.f.	P
Microcavia australis	52.83 (9.35)			
Graomysgriseoflavus	8.01 (3.54)	10.2	1	**0.001**
Akodon molinae	2.39 (4.34)	22.1	1	**0.001**
Eligmodontia typus	31.71 (8.58)	1.6	1	0.2
Calomys musculinus	5.90 (4.34)	10.3	1	**0.001**

Results of Wald test using *Microcavia australis* as intercept are shown. Significant results ($P < 0.05$) are indicated in bold. Data on sigmodontine rodents are from Giannoni *et al.* (2013).

removed mainly by a seed predator, as was suggested by Giannoni *et al.* (2013). During the fruiting period, removal of *P. flexuosa* fruits by small rodents in general decreased and, even though several rodents removed fruits, both *G. griseoflavus* and *M. australis* were still the most important *P. flexuosa* fruit removers. Our findings agree with results obtained in neotropical forests focused on food hoarding by rodents during seasonal fluctuations in food abundance (Feer & Forget 2002). They found that when fruit resources are scarce, before and after peak fruit fall, removal and consumption of fallen fruits and seeds are more pronounced than when fruit abundance increases; in the latter case, animals probably become satiated and remove a decreasing amount of all seeds and fruits available (Feer & Forget 2002).

Microcavia australis transported *P. flexuosa* seeds to short distances, in agreement with many other studies of scatter-hoarding by small rodents and marsupials in a variety of habitats (Sork 1984; Jensen & Nielsen 1986; Dennis 2003; Cheng *et al.* 2005; Campos *et al.* 2007). According to the laboratory results, *M. australis* both larder-hoarded and scatter-hoarded fruits and seeds, but most seeds were cached in scatter-hoards. We found a lower proportion of seeds in scatter-hoards in the field experiment than in the laboratory. This discrepancy could be explained by our reduced capacity for cache detection due to the vegetation cover. Also, during the experiment, we observed ants carrying seeds removed from *M. australis* caches, suggesting the beginning of a new seed dispersal event that could have the potential for furthering seed movements, probably offering different benefits to the tree. It is known that ants remove *P. flexuosa* seeds from different sources such as cattle dung (Velez *et al.* 2016) or *Ctenomys*' mounds (Campos & Velez 2015).

Caches scatter-hoarded by *M. australis* in natural conditions contained few seeds left on the soil surface, a condition that was considered advantageous for seed dispersal (Vander Wall 1990). Comparing the proportion of living seeds left in scatter-hoards by sigmodontine rodents and *M. australis*, results showed similar proportions in caches of *E. typus* and *M. australis*. But differing from *M. australis*, which did not predate seeds, *E. typus* consumed seeds in scatter-hoards and at the food source (Giannoni *et al.* 2013). Importantly though, *E. typus* is unlikely to play a relevant role in the dispersal/predation of *Prosopis* seed because this species is more closely associated with sand dune areas than with *Prosopis* woodland (Corbalán & Ojeda 2004) and our field results showed no fruit removal by *E. typus*.

Different land uses and management strategies practiced in drylands produce changes in richness, abundance and functional diversity of mammals (Chillo & Ojeda 2012; Tabeni *et al.* 2013; Chillo *et al.*

2015; Periago *et al.* 2015). Considering that *M. australis* occupies mainly habitats under grazing management where the vegetation structure allows it to build colonies under plants with an umbrella-like pattern (Tognelli *et al.* 1995), this association of *M. australis* with grazing fields (Tabeni *et al.* 2013) could help maintain the *P. flexuosa* tree populations under anthropogenic disturbance. *Microcavia australis,* through consuming fruits, moving seed to short distances and releasing them from the fruit, could represent an initial mode of *P. flexuosa* seed dispersal at low cost to seeds in comparison with sigmodontine rodents.

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