Seed Science Research (2017), page 1 of 9
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doi:10.1017/S0960258517000101

Seed removal by different functional mammal groups in a protected and grazed landscape of the Monte, Argentina

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(Received 18 July 2016; accepted after revision 20 February 2017)

Abstract

Mammal species contribute in different ways to seed dispersal effectiveness, acting as endozoochorous dispersers, scatter-hoarders and seed predators. Seed removal by these functional mammal groups could be affected by anthropogenic drivers, such as grazing management, a common practice in drylands. We evaluated removal of seeds from a native tree species (*Prosopis flexuosa*) by terrestrial wildlife mammals with different functional roles, on grazed and ungrazed sites and at different times during the fruiting period *of Prosopis*. We offered *Prosopis* fruits, each containing 15 seeds, to animals and used camera traps to identify the species removing them. We obtained the number of seeds removed (1 fruit removed = 15 seeds removed) by each animal species and each functional group. Native and domestic mammals removed 65.4% of the total seeds offered; 69.5% of offered seeds were removed from the grazed area and 61% from the ungrazed site. Considering removal times, 64.25% of offered seeds were removed during the beginning of the fruiting period of *Prosopis* and 67% towards the end of this period. Small mammals acting either as seed predators (*Graomys griseoflavus* and *Akodon dolores*) or scatter-hoarders (*Microcavia australis*) were the functional mammal groups removing the highest amount of seeds. Seed predators removed more seeds from the ungrazed site, whereas the scatter-hoarder did so at the grazed site. In the ungrazed area, it would be important to ensure habitat heterogeneity in order to improve seed removal by functional groups that disperse seeds, such as endozoochorous dispersers and scatter-hoarders.

Keywords: drylands, grazing, mesquite woodland, scatter-hoarders, seed predators

Introduction

In drylands, anthropogenic disturbances such as logging, fire, agricultural expansion, and livestock grazing practices can result in loss of habitat and connectivity, with consequent biodiversity losses (Jones, 2000; Asner *et al*., 2003; Millennium Ecosystem Assessment, 2005; Reynolds *et al*., 2007), and reduction of animal functional diversity (Chillo and Ojeda, 2012; Periago *et al*., 2014). In Argentina's drylands, where grazing by domestic animals is the main land use, most studies have focused on the effect of this disturbance on animal populations (e.g. species decrease in abundance at grazed sites) and its impact at the community level (i.e. habitat modifications, such as an increase in bare ground cover, and their impacts on different species' populations) (Tabeni and Ojeda, 2003, 2005; Corbalán, 2006; Tabeni *et al*., 2007; Rodríguez, 2009). However, little is known about the effects of grazing on biological interactions, such as seed dispersal by animals.

Seed dispersal is crucial for plant populations because it allows new individuals to move away from their mother plant (escape hypothesis; Connell, 1971; Janzen, 1971), explore new areas (colonization hypothesis; Howe and Smallwood, 1982; Nathan, 2006) and regenerate the population (Forget *et al*., 2001; Jordano *et al*., 2011). Animal species can contribute differently to the overall effectiveness of seed dispersal a plant receives from its assemblage of dispersal agents (Schupp *et al*., 2010), among them mammals. Some are endozoochorous dispersers, considered efficient primary seed dispersers that ingest the whole fruit and then defecate or regurgitate the seeds (Janzen, 1983; Jordano, 2000; Forget and Cuijpers, 2008; Vander Wall and Beck, 2012). Other mammal species, mainly rodents, are scatter-hoarders who store seeds in a large number of small caches in the ground for future consumption (Vander Wall and Beck, 2012); and as they eat some seeds but not all of them, they become potential seed dispersers (Vander Wall, 1990, 2002; Forget *et al*., 2002). In contrast, some hoarding species are mainly seed predators, because they store food in underground caches, generally in unfavourable

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conditions for seed germination and seedling establishment (larder-hoarders; Longland *et al*., 2001; Vander Wall and Beck, 2012).

In this context, we conducted a study in a protected area (Ñacuñán Reserve) surrounded by cattle range areas dominated by *Prosopis flexuosa* ('algarrobo dulce') woodland in a dryland biome of Argentina. Mammals removing *P. flexuosa* fruits provide different effectiveness to this tree species (Campos and Ojeda, 1997; Campos *et al*., 2007, 2008; Campos and Velez, 2015). Particularly wildlife species, some are opportunistic frugivores that disperse seeds through endozoochory (e.g. *Lycalopex griseus, Dolichotis patagonum*; Campos and Ojeda, 1997; Campos *et al*., 2008; Campos and Velez, 2015), whereas small rodents behave as scatter-hoarders (*Microcavia australis, Eligmodontia typus*; Giannoni *et al*., 2001, 2013; Campos and Velez, 2015; Campos *et al*., 2017) or seed predators through larder-hoarding (*Graomys griseoflavus, Akodon dolores*; Giannoni *et al*., 2013).

We focused on studying the effects of cattle grazing activity on *P. flexuosa* seed removal by terrestrial wildlife mammals at two times of the fruiting period. We had the following questions: (1) does grazing affect total seed removal by mammals?; (2) is there any temporal difference in total seed removal during different times of the fruiting period of *Prosopis*?; and (3) are there any differences in seed removal by different functional mammal groups between the grazed and ungrazed sites during the beginning and by the end of the fruiting period? If the ungrazed site is functioning as a conservation site, we expected a higher total seed removal in ungrazed than in grazed woodland, because undisturbed woodland provides mammals with more food and refuge (Tabeni and Ojeda, 2005; Corbalán, 2006). Because two different time periods were considered, we expected a high total seed removal at the end of the fruiting period, after peak fruit fall, when removal and consumption of fallen fruits and seeds are usually more pronounced (Janzen, 1974; López de Casenave *et al*., 1998). Finally, we expected that seed removal by the functional mammal groups in both grazed and ungrazed woodlands would be different at different times of the fruiting period due to their natural population fluctuations and habitat preferences (Corbalán and Ojeda, 2004; Tabeni and Ojeda, 2005). In the study area, bare ground cover is higher at the grazed site than in the protected woodland (Tabeni and Ojeda, 2005) and, while some native mammals that disperse *Prosopis* seeds, such as *M. australis* and *D. patagonum*, are associated with open habitats in the cattle-grazed woodland (Tabeni and Ojeda, 2003; Rodríguez, 2009), and *L. griseus* prefers open shrubby areas (Jiménez *et al*., 2008), other species (*G. griseoflavus* and *A. dolores)* are more abundant in areas with dense plant cover such as the protected woodland (Tabeni and Ojeda, 2003, 2005; Corbalán, 2006).

Materials and methods

Study site

This study was conducted in the Man and Biosphere Ñacuñán Reserve (34°02′S, 67°58′W, 12,800 ha; Mendoza Province, Argentina) and in an adjoining cattle ranching area (both 540 m elevation); these sites are located in the Monte biogeographic province (central Monte; Cabrera, 1971; Roig *et al*., 2009). The climate is semi-arid, with cold dry winters (–13 to 10°C) and warm rainy summers (20 to 42°C). Average annual rainfall is 329.4 mm (Estrella *et al*., 2001). Three main types of plant communities occur in the area: mesquite woodland, creosotebush scrubland, and sand dunes (Roig, 1971). The mesquite woodland is the most representative community; it consists of a tree layer of *P. flexuosa* and *Geoffroea decorticans* (mean canopy height being 7 m), a shrub layer with dominance of *Larrea divaricata, L. cuneifolia* and *Condalia microphylla*, and a grass layer of *Pappophorum* spp. *Trichloris crinita* and *Digitaria californica* (Roig, 1971).

At the beginning of the nineteenth century, the area of Ñacuñán suffered severe logging of mesquite woodland and cattle overgrazing (Abraham and Prieto, 1999; Rojas *et al*., 2009). The reserve was established by law in 1961 with the aim of protecting the mesquite woodland (Roig, 1971), and it was fenced in 1972. This reserve offers a unique situation for research because it is the only area in the Monte where grazing by domestic animals is excluded. The adjoining grazed field is under continuous grazing and also presents other related activities (firewood extraction, subsistence hunting, and establishment of watering points, fences, roads and human settlements). Due to environmental constraints in these rangelands, 20 ha/AU (hectares per animal unit) is a commonly used stocking rate (Guevara *et al*., 2009). Previous studies in the area showed greater abundance of adult *P. flexuosa* trees in ungrazed than in grazed woodlands (62 and 32 trees in 0.4 ha, respectively; Aschero and Vázquez, 2009).

Tree species

The study tree, *P. flexuosa* (Fabaceae, Mimosoideae), is a key species in its natural distribution range (Álvarez and Villagra, 2009; Álvarez *et al*., 2011; Campos and Velez, 2015); it provides the human population with services such as shade and valuable goods like wood and food (Ladio and Lozada, 2009).

Prosopis flexuosa blooms in spring (October to December) and fruits start to ripen in summer (February). When the ripe fruits fall, their persistence beneath tree canopies is short because animals remove most of the fruits and seeds within no more than six weeks after they reach the ground (Villagra *et al*., 2002;

Table 1. List of mammal species that removed *Prosopis* seeds and number of cameras by which species was observed at least once at grazed and ungrazed sites and during the beginning and end of the fruiting period

Species	Role	Number of cameras	Grazed site		Ungrazed site	
			Beginning	End	Beginning	End
Akodon dolores	SP	1	0	0	0	1
Chaetophractus vellerosus	UNK	7	5	0	2	0
Conepatus chinga	UNK	1	0	0	1	0
Ctenomys mendocinus	UNK	1	0	0	1	0
Dolichotis patagonum	ED	6	4	0	2	0
Graomys griseoflavus	SP	64	16	11	21	16
Lycalopex griseus	ED	24	11	6	0	7
Microcavia australis	SH	52	27	6	16	3
Cow	ED	13	10	3	–	–
Horse	ED	3	3	0	–	–

Functional groups are: SP (seed predator), UNK ('unknown'), ED (endozoochorous disperser) and SH (scatter-hoarder).

Campos *et al.*, 2007). The fruit is an indehiscent pod, with a relatively soft exocarp (Burkart, 1976) and a thick mesocarp that contains the major portion of sugars and proteins (Kingsolver *et al.*, 1977). Seeds are covered by a bony endocarp and a coat that acts as a barrier inhibiting germination (Warrag, 1994). Germination is accelerated by the passage of seeds through the digestive tracts of animals, with some costs to seed viability (Campos and Ojeda, 1997; Campos *et al.*, 2008).

Seed removal experiment

We randomly chose adult *Prosopis* trees separated by a minimum distance of 500 m, both in the protected and the grazed area. Below the canopy of each tree, we placed 20 *Prosopis* fruits containing 15 seeds each ($n =$ 300 total seeds per tree). Over a 48-h period, we monitored seed removal and the identity of the mammal species removing seeds from beneath each tree using camera traps (Moultrie, M-900i) mounted on trees at a height of 1.80 m. The supply of whole fruits and the short fruit exposure time helped us prevent fruit removal by ants (C.M. Campos, personal observation). The cameras took three consecutive pictures whenever animal movement was detected, with a 30-s delay between shoots. The location of the cameras allowed us not only to identify animal species, but also to count the number of remaining fruits after the animal had left the place (Grünewald *et al.*, 2010). We offered whole *Prosopis* fruits and, as seeds can be counted, we used the number of seeds removed by species and by functional mammal groups as response variable in the model (see 'Data analysis' section). Those seeds that had been moved by an animal far from the camera trap's field of view were considered removed.

To assess whether seed removal by mammals changed at two different times during the fruiting period of *P. flexuosa*, we conducted the experiment at the beginning of the fruiting period when fruits can be found on the ground beneath the trees (March 2015), and by the end of the fruiting period when almost no fruits are available on the ground (May 2015). The production of *Prosopis* fruit is highly variable between years, depending on environmental factors (Dalmasso and Anconetani, 1993; Álvarez and Villagra, 2009). A period of low fruit production has been observed from 2013 onwards (C.M. Campos, personal observation).

Data analysis

Because of the small sample size, we did not include in the model those species with an unknown effect on *Prosopis* seeds ('unknown' group; see Table 1). As our objective was to compare the effect of cattle grazing activity on seed removal by wild mammals, we also excluded from the analysis data on trees from which seeds were removed by domestic animals. After excluding these trees, the final number of camera traps placed on trees at the beginning of the fruiting period was 40 for protected and 47 for grazed sites; and at the end of the fruiting period it was 20 for protected and 17 for grazed sites.

The total number of seeds removed by each species, pooling across individual visits at every tree (response variable), was considered an estimator of the quantity component of seed dispersal effectiveness (Schupp *et al.*, 2010). The variables considered in our model were: site (with two levels: ungrazed and grazed), fruiting time of *P. flexuosa* (with two levels: beginning and end) and functional group [with three levels: seed predator (SP), scatter-hoarder (SH) and endozoochorous disperser (ED)], and interactions between them. The sign of parameters having significant effects

Table 2. Results of zero-hurdle model of seeds removed per site (grazed and ungrazed), times during the fruiting period of *Prosopis* (beginning and end), by different functional groups (FG) of terrestrial mammals (SP: seed predator, ED: endozoochorous disperser and SH: scatter-hoarder) and interactions among variables

Adjusted model	Coefficient	Estimate	SE	*Z*-value	*P*-value
FG×time + FG×site	Intercept	5.46	0.16	32.19	**<0.001**
	Grazed site	−0.37	0.19	−1.88	0.05
	Beginning	−0.37	0.19	−1.91	0.05
	ED	−0.65	0.36	−1.80	0.07
	SH	−0.69	0.34	−1.97	**0.04**
	ED: beginning	0.35	0.37	0.94	0.34
	SH: beginning	1.87	0.55	3.37	**0.0007**
	SP: end	0.67	0.35	1.92	**0.04**
	ED: grazed	0.69	0.37	1.88	0.05
	SH: grazed	0.78	0.29	2.64	**0.008**
	SP: ungrazed	0.79	0.29	2.64	**0.008**

SE, standard error. Significant differences at $P < 0.05$ are in bold.

was used to interpret the results (McCulloch and Searle, 2001; Bolker *et al.*, 2009).

To assess whether seed removal by mammals differed between sites (question 1), between different times during the fruiting period of *Prosopis* (question 2), and among the functional mammal groups at both sites during each time of the fruiting period (question 3), we fitted a generalized linear model (GLM) with a Poisson error structure (McCullagh and Nelder, 1989). As we detected a higher amount of zeros than expected for a Poisson distribution, we fitted a zero-inflated model. Following the model building and selection guidelines by Zuur *et al.* (2009), we obtained and compared the AIC (Akaike information criterion; Akaike, 1981) values from zero-inflated and zero-altered (hurdle) models. Both kinds of models were built with a Poisson and a negative binomial distribution to correct overdispersion. The model we finally chose was the zero-altered negative binomial model (Zeileis *et al.*, 2008; Zuur *et al.*, 2009), which was the one with the lowest AIC value. We included a random tree effect in the model in order to account for pseudoreplication among visits of each species to a tree (Zuur *et al.*, 2009).

All statistical analyses and graphs were performed using R 3.3.1 language and environment (R Development Core Team, 2016). We used the *hurdle*() function from the 'pscl' package for the building of a zero-altered negative binomial model (Zeileis *et al.*, 2008).

Results

During the 280 camera-trap nights (200 for the beginning and 80 for the end of the fruiting period), 65.4% ($n = 24{,}315$) of the total seeds offered ($n = 37{,}200$) were removed, with mammals being the only seed removers. We recorded ten species removing *Prosopis* seed, with *G. griseoflavus*, *M. australis* and *L. griseus* being the species recorded (at least once) by the highest number of camera traps (Table 1). Results on domestic mammals are provided for information purposes only. Cows and horses removed seeds from 16 *Prosopis* trees (Table 1); whereas cows removed seeds during the beginning and end of the fruiting period (mean ± SE number of removed seeds was 26.54 ± 8.4 and 21.75 ± 15.83, respectively), horses were only recorded during the beginning of the period (13.08 ± 7.27).

Regarding our first question, 69.5% of offered seeds were removed from the grazed area and 61% from the ungrazed site. Pooling across all species, there was no difference between sites in total number of seeds removed ($Z = -1.88$; $P = 0.5$: Table 2). Considering times, 64.25% of offered seeds were removed during the beginning of the fruiting period and 67% at the end. There was no statistically significant difference in the number of total seeds removed between times ($Z = -1.91$; $P = 0.5$; Table 2).

The number of seeds removed by different functional mammal groups varied within sites and between times during the *Prosopis* fruiting season (Table 2). The total number of seeds removed by seed predators and by the scatter-hoarder was higher than that removed by endozoochorous dispersers (Tables 2 and 3; Fig. 1). Considering groups with the highest number of *Prosopis* seed removed (seed predators and scatter-hoarder), the model showed site-related differences during the fruiting period of *Prosopis*. The total number of seeds removed by seed predator species was higher at the end of the period and at the ungrazed site, whereas the total number of seed removed by the scatter-hoarder was higher during the beginning of the fruiting period and at the grazed site (Table 2; Fig. 1).

Discussion

Regarding our predictions, we expected a higher total seed removal by wild mammals at the ungrazed site

Table 3. Mean number ± SE of seeds removed and number of visits of each mammal species, and mean number ± SE of seeds removed from both sites (grazed and ungrazed) and times (beginning and end) during the fruiting period

Role	Species	Total seeds removed	Total number of visits	Grazed site		Ungrazed site	
				Beginning	End	Beginning	End
SP	*Graomys griseoflavus*	14.42 ± 1.84	2.84 ± 0.39	7.32 ± 1.77	15.65 ± 3.8	21 ± 5	22 ± 3
	Akodon dolores	0.11	0.01	0	0	0	0.75
SH	*Microcavia australis*	18.08 ± 2.56	1.61 ± 0.23	24 ± 4	10.7 ± 4.7	20 ± 5	3.34 ± 1.9
ED	*Lycalopex griseus*	14.59 ± 3.35	0.32 ± 0.07	16 ± 5.5	26.5 ± 10	8 ± 4	12 ± 7
	Dolichotis patagonum	2.68 ± 1.16	0.09 ± 0.04	4.25 ± 2.27	0	3 ± 2	0
UNK	*Chaetophractus vellerosus*	2.41 ± 1.13	0.06 ± 0.03	3.38 ± 1.71	0	3.38 ± 3	0
	Conepatus chinga	0.32	0.01	0	0	1.13	0
	Ctenomys mendocinus	0.32	0.01	0	0	1.13	0

and at the end of the fruiting period but, contrary to expectations, total seed removal did not differ between grazed and ungrazed sites or between times. However, we did find differences in the number of seeds removed between the functional mammal groups at the different times studied and at both sites.

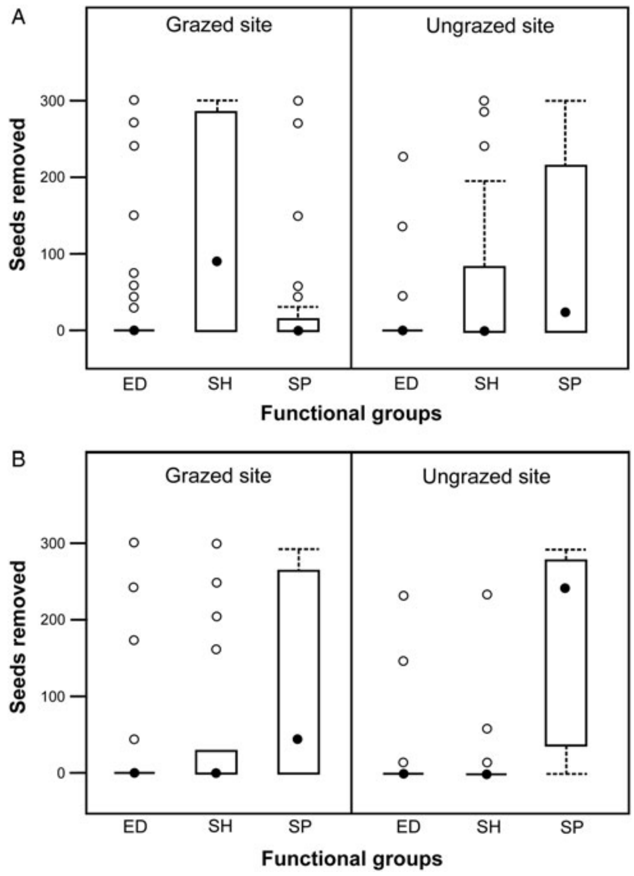

Figure 1. Boxplots of seeds removed per functional group at grazed and ungrazed sites during (A) the beginning and (B) the end of the fruiting period of *Prosopis*. Functional groups are: ED (endozoochorous disperser), SH (scatter-hoarder) and SP (seed predator).

By using camera traps, we were able to identify wild mammal species removing fruits, quantify the number of visits, and estimate the number of *Prosopis* seeds removed by each species. As a result, we found that species recorded by the highest number of camera traps (*G. griseoflavus*, *M. australis* and *L. griseus*; Table 1) had the highest number of feeding visits to the trees and also removed the highest amount of seeds (Table 3). Mammals with an 'unknown' contribution to the *Prosopis* seed dispersal effectiveness were recorded by a lower number of cameras than small and medium-sized mammal species.

The role of small rodents as being responsible for most of the seed removal was previously reported for the Neotropics (e.g. Sánchez-Cordero and Martínez-Gallardo, 1998; Iob and Vieira, 2008). It is also known that, in drylands around the world, invertebrates and small rodents are the main groups removing seeds and acting as seed predators or seed dispersers (Abramsky, 1983; Linzey and Washok, 2000; Marone *et al*., 2000; Kelt *et al*., 2004). Consistent with this general description, results from our study site showed that the main functional mammal groups removing *Prosopis* seeds were small rodents: two sigmodontine species (seed predators; *G. griseoflavus* and *A. dolores*) and one hystricognath species (scatter-hoarder; *M. australis*). Seed removal by medium-sized mammals (*L. griseus* and *D. patagonum*; Table 1) was lower than that by small rodents.

Endozoochorous dispersers such as *L. griseus* and *D. patagonum* play an active role in dispersing *Prosopis* seeds (Campos and Ojeda, 1997; Campos *et al*., 2008); however, none of these species feed exclusively on *Prosopis* fruits. Also, both species are associated with open habitats (Jiménez *et al*., 2008; Rodríguez, 2009). Following their habitat requirements, and despite seed removal by this functional group not being statistically different between sites in our study, we found a tendency towards a higher number of trees visited (Table 1) and a higher number of seed removed (Table 2) by these medium-sized mammals, particularly by *L. griseus*, at the grazed site compared with the ungrazed site. The tendency found here indicates a high seed removal activity of these native species at a site where they could be more exposed to risks from human activities, thereby increasing their vulnerability to being hunted (Campos *et al.*, 2001; Tabeni *et al.*, 2013).

During the beginning of the fruiting period of *Prosopis*, the seed predators (*G. griseoflavus* and *A. dolores*) at the ungrazed site and the scatter-hoarder (*M. australis*) at the grazed site were the main functional groups removing seeds. Following our predictions, these results could be related to the habitat requirements of the species. From previous studies we know that grazing by large herbivores causes habitat modifications such as alteration of biomass and vegetation structure with consequent effects on small-sized mammal populations (Jones, 2000; Flowerdew and Ellwood, 2001; Foster *et al.*, 2014). In the central Monte, the main seed predator *G. griseoflavus* avoids open habitats and is associated with patches of complex vegetation structure on grazed and ungrazed sites (Tabeni *et al.*, 2007). *Akodon dolores*, which only removed a low number of seeds from the ungrazed site during the end of the fruiting period (Tables 1 and 3), prefers habitats with high plant density inside the ungrazed area (Tabeni and Ojeda, 2005; Corbalán, 2006). In contrast, *M. australis*, which removed a higher number of seeds from the grazed site, mainly occupies habitats under grazing where vegetation structure allows it to build its colonies under plants with an umbrella-like pattern (Tognelli *et al.*, 1995).

Despite the different number of trees included in our experiment at both fruiting times considered, we found strong tendencies of differential seed removal by mammals on sites under two land management practices. During the end of the period, the seed predator group removed the highest number of seeds. This could be related to the seasonal increase in the population abundance of *G. griseoflavus* occurring in autumn (Ojeda, 1989; Corbalán and Ojeda, 2004). As an advantage from the seed point of view, the time when the peak fall of *Prosopis* fruits occurs (summer) does not coincide with the time at which the population of their main seed predator is naturally more abundant (autumn).

Our results represent a season of low *Prosopis* fruit production, considering the high inter-annual variability in crop size of this tree species (Dalmasso and Anconetani, 1993). However, the dynamics of seed removal by mammals found here may vary in a year of higher fruit availability; in that case, mammals may or may not become satiated by large fruit production events (Kelly and Sork, 2002). Also, a previous study in the area found *Prosopis* seed production to be higher at the protected than grazed sites (Aschero and Vázquez, 2009). Further research in a year of high *Prosopis* fruit production could explain the seed removal response by mammals in an ecological context of different fruit availability.

In summary, seed predator species removed more seeds compared with other species at the ungrazed site and during the end of the fruiting period, whereas the scatter-hoarding species removed more seeds from the grazed site at the beginning of the period. On the one hand, the nearly 50-year exclusion of large herbivores from the protected area seems to have generated more suitable microhabitats for seed predators and to have caused the expulsion of medium-sized mammals (Tabeni *et al.*, 2013). On the other hand, grazing management could be advantageous for seed removal by a hoarding species and by medium-sized mammals that disperse seeds through endozoochory. Nevertheless, a lower percentage of *Prosopis* seedling survival was reported for the grazed area compared with the ungrazed site, probably due to intensive cattle trampling (Campos *et al.*, 2011; Aschero *et al.*, 2016). As a first approach to addressing seed removal by mammals using camera traps, and from a plant perspective, a tentative suggestion would be to maintain, in the protected area, a heterogeneity of habitats that ensures that all local wildlife species play their functional roles (Campos *et al.*, 2016), mainly enlarging the habitat associated with seed disperser species.

Acknowledgements

The authors thank all the staff of Ñacuñán Reserve for their cooperation; and the owner and the family in charge for allowing us to work in the cattle ranching area. We also thank three reviewers for comments on an earlier version of the manuscript. Nélida Horak assisted us in drafting the English version.

Financial support

This work was supported by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET-PIP 112-201101-00601), Agencia Nacional de Promoción Científica y Tecnológica (PICT-2013-0478) and a graduate fellowship from CONICET to F.M.

Conflicts of interest

None.

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