

# Endozoochory by native and exotic herbivores in dry areas: consequences for germination and survival of *Prosopis* seeds

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## Abstract

Mammalian herbivores can play a role in the endozoochorous dispersal of *Prosopis* seeds in the arid zones of Argentina, and the introduction of exotic mammals can change relevant parameters of the plant's reproductive ecology. Our specific goals were to quantify the seeds of *Prosopis flexuosa*, *P. chilensis* and *P. torquata* contained in the faeces of native [mara (*Dolichotis patagonum*), guanaco (*Lama guanicoe*)] and exotic [donkey (*Equus asinus*) and hare (*Lepus europaeus*)] mammals, and to determine the mortality, germination percentage and germination speed of seeds borne in faeces, compared with those collected from trees. In 2006, seeds were collected directly from trees or removed from mammal faeces. Seeds were counted and classified as apparently healthy or damaged. *P. torquata* and *P. flexuosa* seeds were found in the dung of guanaco, hare and mara, whereas only *P. flexuosa* seeds appeared in donkey faeces. *P. chilensis* seeds were only found in guanaco faeces. There was a notable relative abundance of seeds contained in small herbivore faeces in comparison to the large herbivores. The passage through the digestive tract of animals modified seed germination capacity and speed, with great variability between animal species. Guanacos had greater effects than donkeys on mortality, germination percentage and germination speed. Differences between the effects of both smaller-sized herbivores on seeds were much smaller.

**Keywords:** Argentina, desert, donkey, guanaco, hare, Ischigualasto, mara, mesquite, *Prosopis*

## Introduction

Biological processes, such as endozoochory, involve the ingestion of seeds and their passage through the animal digestive tract. Seeds can be scarified, increasing germination speed, although the mortality potential increases if the seed coats weaken too much (Janzen *et al.*, 1985). These effects of herbivory are related to digestion, the gut retention period, seed size and the hardness of seed coats according to the maturity stage of propagules, etc. (Janzen, 1981, 1982; Janzen *et al.*, 1985). However, enhanced germination of seeds following passage through the herbivore gut may not always be beneficial (Traveset and Verdú, 2002).

The effect of endozoochorous dispersers on seeds also depends on their final destination. On the one hand, seed transport is beneficial for the plant by allowing it to occupy new environments (colonization hypothesis; Howe and Smallwood, 1982) and to reduce predation risk, parasitism and competition near the mother plant (escape hypothesis; Janzen, 1970; but see Hyatt *et al.*, 2003). In some cases faeces can also provide a propitious environment for germination (Gokbulak and Call, 2004). However, final seedling establishment is not ensured, because it depends on seedling and seed predation in the faeces, the suitability of the defecation site for seedlings, sibling competition for resources and the current environmental conditions (Janzen, 1981; Howe, 1986). In view of the complexity of factors involved in endozoochory, it is not surprising that the effects of seed dispersal are sometimes contradictory, with frequent variations between different sites, plants and herbivore species (Traveset and Verdú, 2002; Verdú and Traveset, 2005).

Exotic species can disrupt mutualistic plant–animal interactions such as seed dispersal (Traveset and Riera, 2005). When seed dispersal is a limiting factor, they can be effective seed dispersers of many

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native plants, but they can also have a detrimental effect if they compete with native dispersers and/or modify either the seed shadow or the germination patterns generated by native dispersers (see review by Traveset and Richardson, 2006).

In the semi-arid areas of Argentina, species of the genus *Prosopis* (*Fabaceae*) play an important role in the functioning of plant and animal communities. *Prosopis* acts as an environmental stabilizer and yields a variety of useful products for rural populations. This genus maintains ecosystem complexity by creating microhabitats and is a valuable food resource for both humans and animals (Kingsolver *et al.*, 1977; Mares *et al.*, 1977; Or and Ward, 2003; Rossi and Villagra, 2003). Domestic and wild herbivores can play a role in the endozoochorous dispersal of *Prosopis* seeds (e.g. Eilberg, 1973; Peinetti *et al.*, 1992, 1993; Campos and Ojeda, 1997; Ortega Baes *et al.*, 2002; Kneuper *et al.*, 2003). In this interaction, seeds can lose viability and be subject to different effects on germinability, depending on the particular mammal and *Prosopis* species involved. Results of studies of *P. ruscifolia*, *P. caldenia* and *P. ferox* consider that in animals, such as cows, goats and donkeys, gut passage is not an important means of seed release from dormancy, and therefore endozoochory may not increase germination percentages (Eilberg, 1973; Peinetti *et al.*, 1992; Ortega Baes *et al.*, 2002). However, when other mammals (horses, wild mammals) participate in endozoochory, germination percentages increase significantly (*P. ruscifolia*, *P. caldenia*, *P. flexuosa*, *P. glandulosa*; Eilberg, 1973; Peinetti *et al.*, 1993; Campos and Ojeda, 1997; Kneuper *et al.*, 2003). Therefore, the introduction of exotic herbivores may change *Prosopis* dispersal processes, with potential effects on the function of plant communities in the Monte desert where these species play a major role.

In this context, our specific goals were: (1) to quantify the *P. flexuosa*, *P. chilensis* and *P. torquata* seeds contained in the faeces of native (mara and guanaco) and exotic mammals (donkey and hare); and (2) to determine mortality, germination percentage and germination speed of faeces-borne seeds compared to those collected directly from trees.

## Materials and methods

### Study site

The study was conducted in the Ischigualasto Provincial Park (29°55'S, 68°05'W), 335 km from San Juan city, Valle Fértil Department, at 1300 m above sea level. The region has a desert climate, a wide day/night temperature range, summer rains below 100 mm per year, -10°C absolute minimum in winter and 45°C absolute maximum in summer.

Approximately 90% of the area is part of the Monte phytogeographical province, with small sectors in the Chaco Serrano and the Cardonal districts (Acosta and Murúa, 1999; Márquez, 1999). The predominant physiognomy is open scrubland, with heavy soil and moisture limitations on the plant communities (Márquez, 1999).

Some of the analysed mammalian species have conservation problems due to their restricted geographic distribution and low population densities. Moreover, available information is quite scarce, as in the case of mara (*Dolichotis patagonum*), a hystricognath rodent ranked as requiring 'special attention' (Acosta and Murúa, 1999) and 'vulnerable' (Diaz and Ojeda, 2000), and guanaco (*Lama guanicoe*), ranked as 'potentially vulnerable' (Diaz and Ojeda, 2000). Although it has a wide distribution and flexibility in its use of food resources, guanaco populations are under heavy pressure from poaching and the introduction of alien species (Puig *et al.*, 2001). Recently, the guanaco population in Ischigualasto has been given the 'highest conservation priority' (Acosta and Murúa, 1999). In addition, the Park supports exotic species, such as donkey (*Equus asinus*) and hare (*Lepus europaeus*), whose interactions with vegetation and native mammals are virtually unknown.

### Seed and faeces collection

*Prosopis* fruit is a modified indehiscent legume with a thin epicarp, a mesocarp that can be fleshy, sugary or fibrous and several endocarp segments (Burkart, 1976). *Prosopis* germination is hindered by physical dormancy (Bewley and Black, 1982; Peinetti *et al.*, 1993), and seed scarification by different agents increases germination (Catalán and Balzarini, 1992; Peláez *et al.*, 1992; Peinetti *et al.*, 1993; Ortega Baes *et al.*, 2002).

Between January and April 2006, we collected seed samples of 10 fruits per tree directly from 9, 10 and 11 *P. flexuosa*, *P. chilensis* and *P. torquata* trees, respectively (henceforth tree seeds). During this period, we also collected fresh independent samples of faeces of exotic (donkey and hare) and native mammals (mara and guanaco). Independent faeces samples were defined as those more than 2 m apart for small mammals or 100 m for large mammals. The samples were collected in the habitats used most heavily by the herbivores within a roughly 200 km<sup>2</sup> area.

We counted the *Prosopis* spp. seeds in a total of 574 g of air-dried faeces for mara, 1298 g for guanaco, 32.8 g for hare and 1300 g for donkey, taken from 100, 26, 15 and 13 independent samples, respectively. The seeds were classified as apparently healthy (with and without endocarps) or damaged, based on

observations of external traits. Insect-damaged seeds (presence of insect exit holes) were counted separately from those with other damage (broken by chewing, open endocarps with malformed seed, etc.).

### Germination experiments

During July 2006, germination tests were performed in incubators (Precision GCA Corporation, Scientific Model 818, Chicago, Illinois, USA) with constant light and temperature (30°C), using 9-cm diameter Petri dishes prepared with sand moistened to saturation. Mortality, germination percentage and germination speed were measured for seeds taken from trees (control seeds) and for seeds from herbivore faeces.

We used visually healthy *P. flexuosa*, *P. chilensis* and *P. torquata* seeds with endocarps collected from trees (two 25-seed replicates for each tree). In the case of *P. flexuosa*, two seed lots were used, with and without endocarps, as seeds in both conditions appeared in the faeces. Apparently healthy seeds collected from herbivore droppings were also cultivated, with sample sizes determined by seed availability. Thus, *P. flexuosa* seeds were found in mara faeces and donkey dung (16 replicates of 25 seeds used for each herbivore), hare (3 replicates of 25 seeds each) and guanaco (4 replicates of 25 seeds: 3 replicates of seeds without endocarp and 1 replicate of seeds with endocarp). *P. chilensis* seeds were found only in guanaco faeces (16 replicates of 25 seeds each). *P. torquata* seeds were taken from mara and guanaco faeces (16 replicates of 25 seeds for each herbivore) and hare faeces (3 replicates of 25 seeds).

### Germination percentage and speed

To define the percentage of viable seeds, seeds that had not germinated in the previous experiment were manually scarified and placed under the above-mentioned conditions for 14 d. Scarified seeds that did not germinate after this period were subjected to the standard treatment with a 2,3,5-triphenyl-tetrazolium chloride test (Pili-Sevilla, 1987), which detects seed viability by staining the embryo tissue pink/red.

Germination percentage was the number of germinated seeds in relation to the number of viable seeds known at the end of the trials. Seed mortality was obtained from the number of non-viable seeds in the tests, plus the number of damaged seeds (parasitized by insects, malformations, affected by herbivores, etc.) in relation to the number of seeds in the lots.

Seed germination speed was estimated for all seed sources, and the weighted germination percentage

(germination speed) index was calculated for a 21 d period (Reddy *et al.*, 1985). This index gives maximum weight to the seeds that germinate first and a decreasing weight to subsequent germination. It is computed as follows:

$$\text{Germination speed} = \frac{21n_1 + 19n_3 + \dots + 1n_{21}}{21N} \times 100$$

where  $n_1, n_3, \dots, n_{21}$  = number of seeds germinated on the first, third, ..., twenty-first day, and  $N$  = total number of seeds. The value for germination speed varies between 100 (if all seeds germinate on the first day) and 0 (when none germinate in the study period).

### Statistical analysis

The Kruskal–Wallis test was used to compare mortality, germination percentage and germination speed among seeds from different sources, due to the lack of normality in these variables. *Post hoc* comparisons were performed using the Mann–Whitney test (Zar, 1984) with the sequential Bonferroni correction (Rice, 1989). All statistical analyses were performed with SPSS 13.0 (SPSS Corp., Chicago, Illinois, USA).

### Results

*P. torquata* and *P. flexuosa* seeds were found in guanaco, hare and mara dung, whereas only *P. flexuosa* seeds appeared in donkey faeces (Table 1). *P. chilensis* seeds were found only in guanaco faeces. In general, small herbivore faeces contained higher total densities of *Prosopis* seeds than those of the large herbivores (4–5 seeds  $\text{g}^{-1}$  versus 1–2 seeds  $\text{g}^{-1}$ ).

Table 1 shows that *P. torquata* seeds in dung were generally embedded within their endocarps; however, small numbers without endocarp were found in mara and guanaco dung. In the case of *P. flexuosa*, most seeds occurring in the faeces of mara, hare and donkey were enclosed inside their endocarps. Seeds of *P. chilensis* only appeared in guanaco dung and they lost their endocarps during gut passage.

A surprisingly large number of damaged seeds were found in the faeces of guanaco (for *P. torquata* and *P. chilensis*) and donkey (*P. flexuosa*). Insect damage seemed to be particularly frequent in *P. chilensis* seeds contained in guanaco dung (Table 1).

### Seed mortality

The mortality for *P. torquata* seeds differed significantly between groups ( $K = 34.07$ ,  $P < 0.001$ , Fig. 1a). Seeds in guanaco faeces exhibited the highest

**Table 1.** Seed content (mean  $\pm$  SE) of *Prosopis* species in the faeces of the four herbivores studied. The detected seeds were classified by appearance as healthy (with or without endocarp) or damaged (see text). Data show seeds/10 g of dung, with the relative percentage of each seed class for each species of *Prosopis* and herbivore shown in parentheses

	Mara (N = 100)	Guanaco (N = 26)	Hare (N = 15)	Donkey (N = 13)
<i>P. torquata</i>				
With endocarp	26.45 $\pm$ 2.02 (93.56)	4.58 $\pm$ 1.39 (81.93)	28.65 $\pm$ 6.79 (94.46)	
Without endocarp	0.02 $\pm$ 0.01 (0.07)	0.02 $\pm$ 0.01 (0.36)		
Damaged by insects	1.55 $\pm$ 0.38 (5.48)	0.03 $\pm$ 0.02 (0.54)	0.51 $\pm$ 0.51 (1.68)	
Damaged by other causes	0.25 $\pm$ 0.08 (0.88)	0.96 $\pm$ 0.33 (17.17)	1.17 $\pm$ 0.68 (3.86)	
<i>P. chilensis</i>				
With endocarp				
Without endocarp		10.63 $\pm$ 4.28 (69.25)		
Damaged by insects		4.64 $\pm$ 1.74 (30.23)		
Damaged by other causes		0.08 $\pm$ 0.05 (0.52)		
<i>P. flexuosa</i>				
With endocarp	13.69 $\pm$ 1.47 (82.42)	0.22 $\pm$ 0.08 (20.37)	16.97 $\pm$ 5.89 (77.10)	11.80 $\pm$ 3.54 (54.26)
Without endocarp	0.43 $\pm$ 0.16 (2.58)	0.70 $\pm$ 0.34 (64.81)	1.23 $\pm$ 0.97 (5.59)	0.13 $\pm$ 0.09 (0.60)
Damaged by insects	0.99 $\pm$ 0.25 (5.96)	0.05 $\pm$ 0.04 (4.63)	0.45 $\pm$ 0.31 (2.04)	4.37 $\pm$ 1.00 (20.09)
Damaged by other causes	1.50 $\pm$ 0.26 (9.03)	0.11 $\pm$ 0.04 (10.18)	3.36 $\pm$ 1.16 (15.26)	5.45 $\pm$ 1.57 (25.06)

mortality compared to control seeds, seeds in hare droppings and seeds in mara faeces. The latter three groups showed no significant differences. *P. chilensis* seed mortality was significantly higher in seeds dispersed by guanaco than in control seeds ( $U = 12.5$ ,  $P < 0.001$ , Fig. 1b). Mortality for *P. flexuosa* seeds with endocarps showed significant differences between groups ( $K = 18.12$ ,  $P = 0.001$ , Fig. 1c). Seeds collected from donkey dung exhibited the highest mortality, differing from seeds dispersed by mara and from control seeds. Seeds contained in mara faeces also showed a significantly higher mortality than control seeds, whereas seeds dispersed by hare showed no statistical differences from the other groups. Mean mortality for seeds found in guanaco faeces was generated by only one replicate of 25 seeds, thus preventing comparisons between this and the other groups. The mortality of seeds without endocarps was significantly higher in seeds dispersed by guanaco ( $U = 6.39$ ,  $P = 0.011$ , Fig. 1d) than in control seeds.

### Germination percentage

For *P. torquata*, germination percentage showed no significant differences between groups ( $K = 5.64$ ,  $P = 0.130$ , Fig. 2a). In the case of *P. chilensis*, germination percentage was significantly higher in seeds dispersed by guanaco than in control seeds ( $U = 9$ ,  $P < 0.001$ , Fig. 2b). For *P. flexuosa* seeds with endocarps, germination percentages showed only marginal differences between groups ( $K = 8.17$ ,  $P = 0.08$ , Fig. 2c). Nonetheless, *post hoc* comparisons showed a higher germination percentage in seeds dispersed by hare than in those dispersed by mara. No significant differences were found in any other

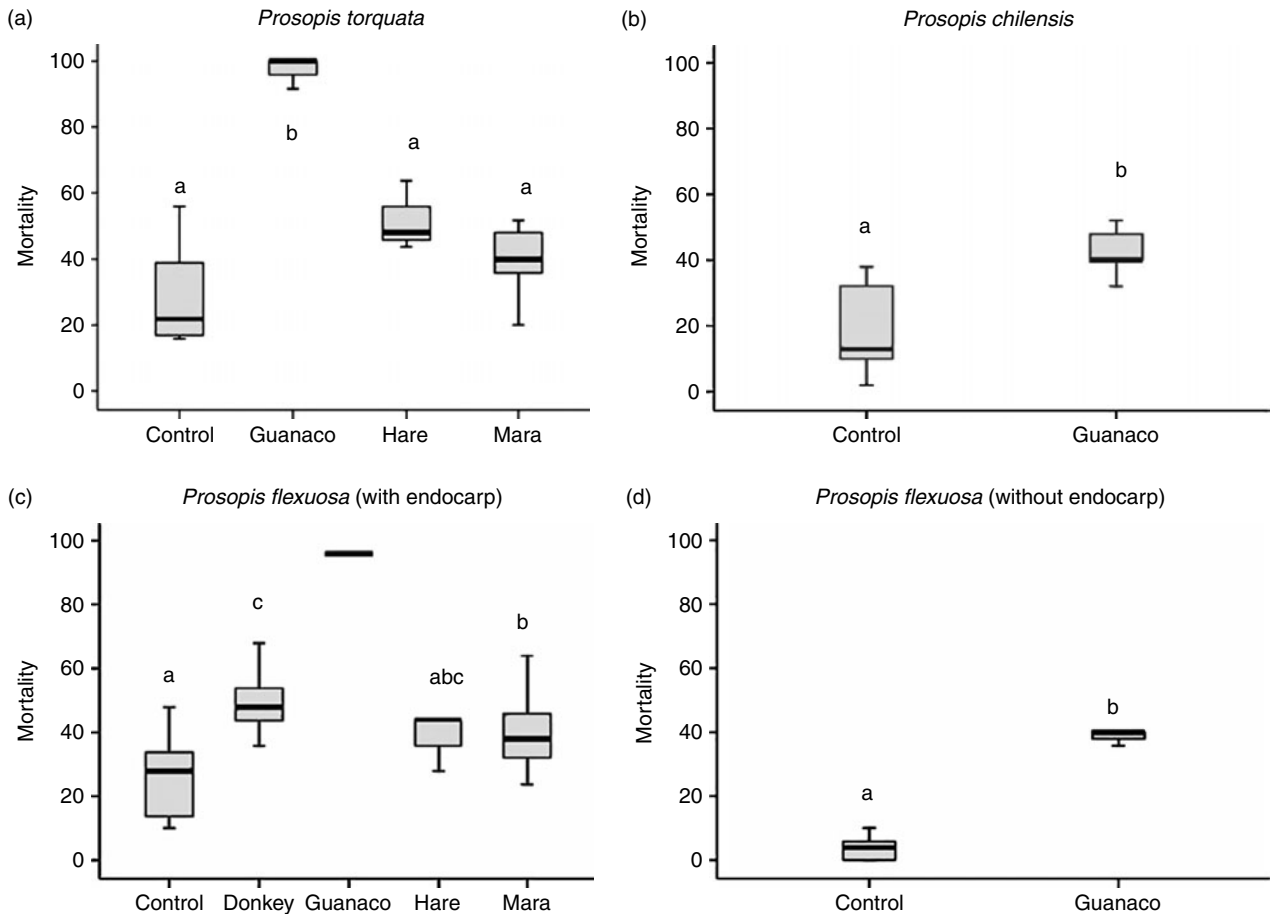
comparisons. *P. flexuosa* seeds without endocarps from guanaco faeces showed a higher germination percentage than the control seeds ( $U = 0$ ,  $P = 0.013$ , Fig. 2d).

### Germination speed

Germination speed for *P. torquata* was significantly different among groups ( $K = 18.2$ ,  $P < 0.001$ , Fig. 3a). Seeds contained in guanaco faeces germinated more slowly than those from mara or hare faeces, but not control seeds. Seeds found in faeces of small herbivores showed a significantly higher germination speed than control seeds. *P. chilensis* germination speed was significantly higher in seeds dispersed by guanaco than in control seeds ( $U = 10$ ,  $P < 0.001$ , Fig. 3b). For *P. flexuosa* seeds with endocarps, germination speed showed differences between groups ( $K = 9.69$ ,  $P = 0.046$ , Fig. 3c). Seeds dispersed by hare showed a higher germination speed than seeds dispersed by donkeys and control seeds. Finally, *P. flexuosa* seeds without endocarps taken from guanaco faeces presented a higher germination speed than control seeds ( $U = 3$ ,  $P = 0.05$ , Fig. 3d).

### Discussion

All herbivores dispersed the seeds of one or more *Prosopis* species through their faeces, and in some cases, the passage of seeds through the animal gut modified their germinability. This is also the first record of dispersal by herbivores of *P. torquata* and *P. chilensis*, two significant species in the arid zones of Argentina (Burkart, 1976).



**Figure 1.** Mortality of seeds (number of dead seeds/number of seeds in lots of 100 seeds) taken from trees (control) and dung of different herbivores for *Prosopis torquata*, *P. chilensis* and *P. flexuosa* (without endocarp and with endocarp). In this and other figures, different letters indicate significant differences between groups (control, donkey, guanaco, hare and mara) after correction for multiple testing (Rice, 1989). Each box shows the range between 25th and 75th percentiles; the central line shows the median. Vertical bars represent the highest and lowest values that are not outliers or extreme values.

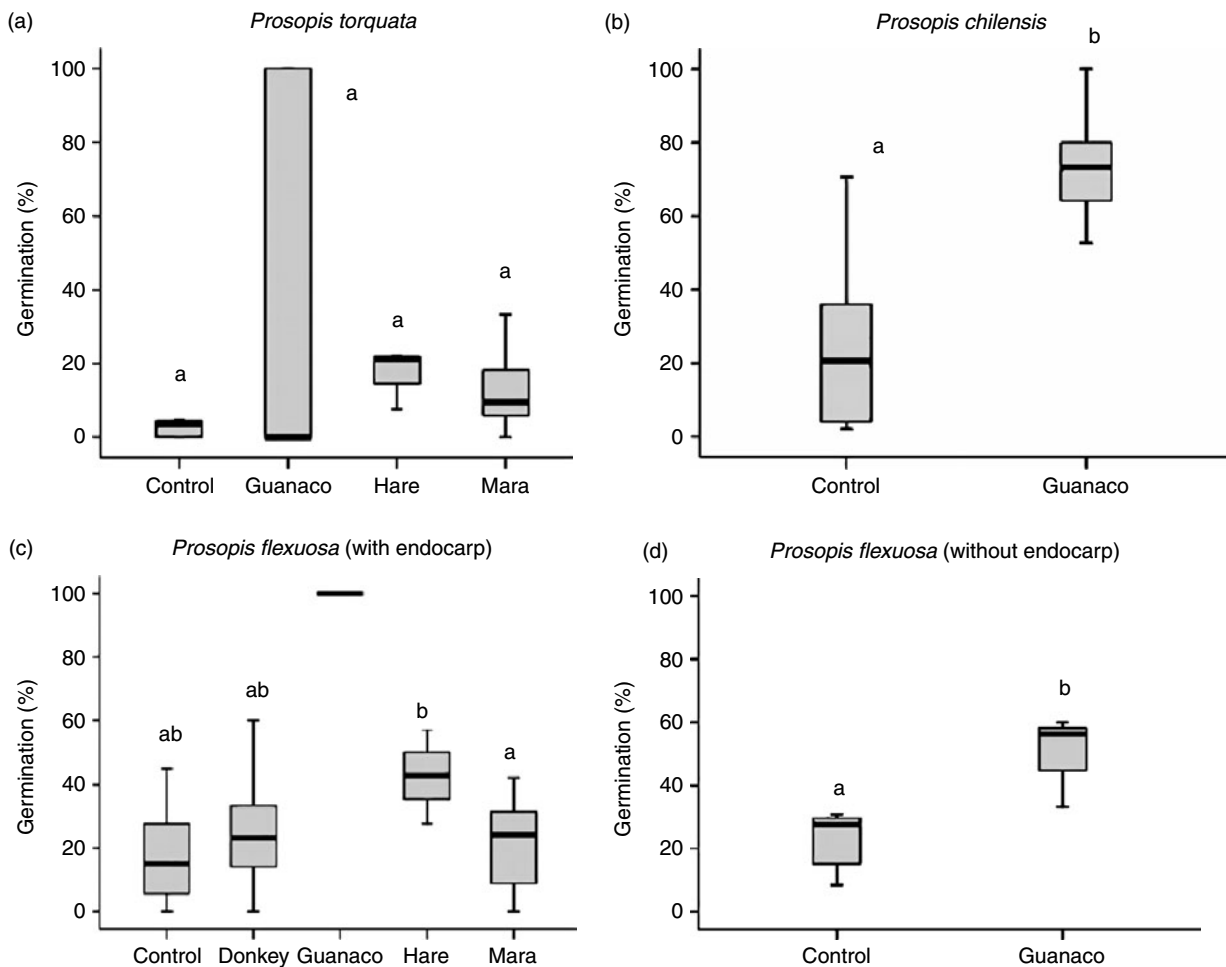
### Seeds in faeces

Considerable numbers of *Prosopis* seeds were found in the faeces of the four analysed small- and large-sized herbivores. Although this has been found on several occasions for various herbivore species (e.g. Campos and Ojeda, 1997; Kneuper *et al.*, 2003; Varela, 2004), the present study is the first one to highlight differences between herbivores, with a special focus on the native versus exotic effect in an extremely arid protected area.

*P. torquata* and *P. flexuosa* seeds were found in high and similar densities in the faeces of the two smallest species. Studies of the trophic ecology of these herbivores show that their behaviour is opportunistic in the consumption of *Prosopis* spp. fruits, when available in large quantities (Campos, 1997; Campos *et al.*, 2001).

Major differences were found in larger herbivores, with a notable presence of all three *Prosopis* species in guanaco faeces, as opposed to the occurrence of only *P. flexuosa* in donkey dung. This undoubtedly reflects the use of a wide diversity of environments by guanacos and their browsing behaviour (Puig *et al.*, 1997, 2001), in contrast to donkeys, which have a feeding strategy that is closer to that of bulk grazers and tend to concentrate around ephemeral watercourses (Lamoot *et al.*, 2005; Acebes *et al.*, unpublished).

Large percentages of damaged seeds were detected in animal faeces, especially in the cases of guanaco (*P. torquata* 18% and *P. chilensis* 31%) and donkey (*P. flexuosa* 45%). Taking only insect damage into account, *P. chilensis* seeds are seriously affected in guanaco faeces (30%) as are *P. flexuosa* seeds in donkey dung (20%). The insect damage data should be used with caution and considered as estimates of the



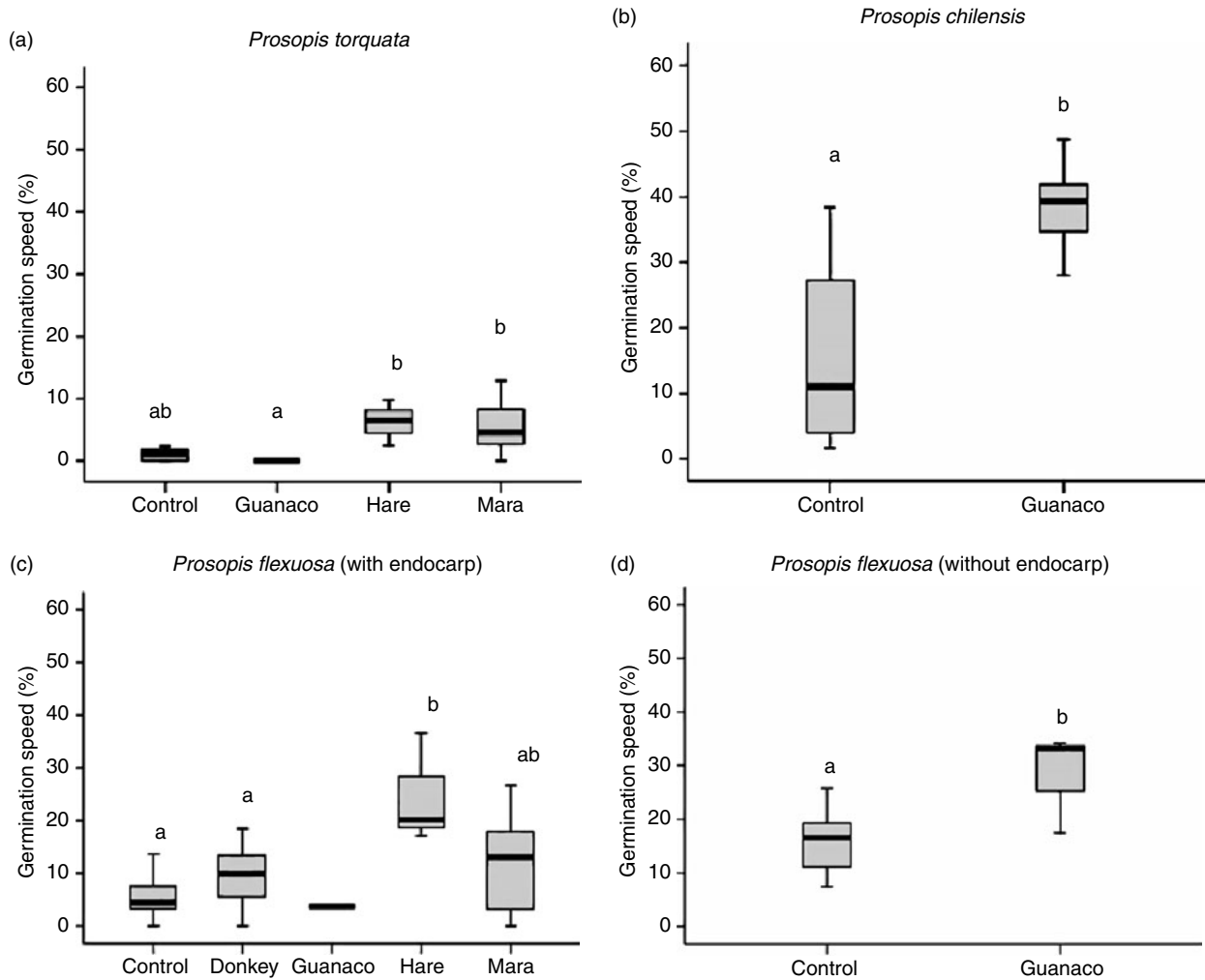
**Figure 2.** Germination percentages of seeds taken from trees (control) and dung of different herbivores for *Prosopis torquata*, *P. chilensis* and *P. flexuosa* (without endocarp and with endocarp). Symbols as in Fig. 1.

minimum number of damaged seeds; they are taken from external observations of holes in the endocarp produced by the emergence of adult insects, while seeds affected by larvae of arthropods and by plant infections were not quantified. This observation matches studies of the *Prosopis* genus that show predation by bruchids is high in both pods in trees (Smith and Ueckert, 1974; Kingsolver *et al.*, 1977) and pods in the soil (Lerner and Peinetti, 1996; Ortega Baes *et al.*, 2001), although our study did not reveal when the seeds were infected. With respect to the number of seeds damaged by other causes, we found a large number in guanaco faeces for *P. torquata* (17%) and in donkey faeces for *P. flexuosa* (25%). High percentages of death among seeds ingested by large herbivores could be associated with the long duration of gut passage, but differences across plant species found in any animal dung are more difficult to interpret, and may be related to pod traits such as dryness.

### **Mortality, germination percentage and speed**

Seed mortality increased following passage through the animal gut, particularly in the case of the two largest herbivores. The change was significant in all cases with the guanaco, increasing in the most extreme situation from 20 to 100% (medians for *P. torquata* seeds). Similarly, passage through the donkey digestive tract increased the mortality of *P. flexuosa* seeds from 28 to 48%, contrary to the results of Ortega Baes *et al.* (2002), who found no effect from consumption by donkey on the viability of *P. ferox* seeds compared to seeds taken from plants.

Among the smallest herbivores, only passage through the mara digestive tract increased mortality in *P. flexuosa* seeds with endocarps, in comparison with control seeds. In a previous study in the Monte desert (Ñacuñán Reserve, Mendoza Province), mortality due to endozoochory by rodents such as mara



**Figure 3.** Germination speed (%) for seeds taken from trees (control) and dung of different herbivores for *Prosopis torquata*, *P. chilensis* and *P. flexuosa* (without endocarp and with endocarp). Symbols as in Fig. 1.

was roughly 30% (Campos and Ojeda, 1997), similar to the results of the present study.

Regarding percentage and speed of germination, comparisons between large herbivores showed that guanaco had larger effects on seeds than donkey, which did not increase either parameter. The low response of passage through the donkey digestive tract is consistent with studies that suggest that intake of *Fabaceae* pods by domestic herbivores (cattle, goat and donkey) does not appear directly to improve seed germinability in some *Prosopis* species (*P. ruscifolia*, *P. caldenia* and *P. ferox*), in comparison with healthy seeds scarified by mechanical or chemical means (Eilberg, 1973; Peinetti *et al.*, 1992, 1993; Ortega Baes *et al.*, 2002; Kneuper *et al.*, 2003). However, the guanaco significantly increased the germinable proportion and germination speed of *P. chilensis* seeds and *P. flexuosa* without endocarps,

although it did not seem to alter these parameters in *P. torquata* seeds. Moreover, in the case of *P. flexuosa*, the seeds found in the faeces had been freed of their endocarps.

Among the smaller herbivores, few effects on germination percentage and speed were detected. Only hare seemed to increase the germination percentage of *P. flexuosa* seeds with endocarps. Previous studies did not find any effect of hare gut passage on germination (Izhaki and Ne'eman, 1997), although the lack of effects may be due to the comparisons having been made between seeds from hare faeces and manually scarified seeds. However, in the Monte desert (Ñacuñán Reserve, Mendoza Province), medium-sized rodents, such as mara, disperse *P. flexuosa* seeds with endocarps and enhance their germination capacity (Campos and Ojeda, 1997).

The effects of herbivore gut passage on *Prosopis* seed survival and germinability are multiple and differentiated between plant species and animal dispersers. Large variability in seed germination capacity and speed after gut passage is usually found in comparisons of endozoochory by different animal species (for reviews see Traveset, 1999; Traveset and Verdú, 2002; Verdú and Traveset, 2005). In our case, this variability was both direct, in terms of survival and germinability, and indirect, via the deposition of a percentage of the seeds released from the endocarp (*P. flexuosa* in guanaco faeces). In this case, gut passage partially released seeds from the physical dormancy imposed by hard impermeable seed coats and should facilitate subsequent environmental scarification by soil abrasion or extreme temperature cycles (Janzen, 1981; Izhaki and Ne'eman, 1997; Ortega Baes *et al.*, 2002). In any case, removal of *P. flexuosa* pods by animals should not be described just as a mechanism for seed loss (Villagra *et al.*, 2002; Milesi and López de Casenave, 2004; Campos *et al.*, 2007), since part of the removed seeds can remain viable and may give rise to the establishment of new plants. The final effect on the plant species depends on the costs associated with the loss of seeds through animal ingestion and digestion, and the effect of seed predators and environmental conditions for germination and establishment on the fate of dispersed seeds (Howe and Smallwood, 1982; Maron and Gardner, 2000). Our data show changes in the seed availability and germinability parameters that determine this final effect, thus introducing the possibility of differential changes in *Prosopis* spp. recruitment linked to the presence of alien herbivores.

Finally, when evaluating the results, we must bear in mind that the experimental conditions can have consequences for the detected effects on the seeds (Rodríguez-Pérez *et al.*, 2005; Samuels and Levey, 2005; Robertson *et al.*, 2006; Traveset *et al.*, 2007). To minimize this problem in the present study, we compared seeds from trees and from faeces not released from endocarps, finding that germinability of control seeds was lower than in previous laboratory studies. However, in many experiments the effect on germinability is measured by comparing dung-borne seeds with healthy control seeds that have been scarified by mechanical or chemical means, which is optimal for breaking dormancy and maximizing germination under laboratory conditions (e.g. Catalán and Macchiavelli, 1991; Catalán and Balzarini, 1992; Coney and Trione, 1996; Ortega Baes *et al.*, 2002).

In conclusion, although the directionality of changes associated with the presence of exotic herbivores is not easy to determine, there is a clear differential effect across herbivores on *Prosopis* spp. seed endozoochory and germination. Moreover, for the two analysed pairs of herbivore species, changes linked to dispersal in dung by hare in comparison to

mara are smaller than those associated with endozoochory by donkey versus guanaco.

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