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Seed predation and removal from faeces in a dry ecosystem

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Abstract

The fate of dispersed seeds from mammal faeces depends both on the animal that finds the seeds and environmental conditions. We explored the simultaneous influence of microhabitat and food availability on seed predation and removal from faeces by different animals in a protected *Prosopis flexuosa* open woodland site of the central Monte desert (Argentina). Using exclusion trials on simulated cattle faeces, we quantified seed predation *in situ* (within cages) and seed removal from faeces by rodents and ants in two different microhabitats (under shrub cover and on bare soil). This was done for two levels of availability of *P. flexuosa* fruits (during the fruiting season of *P. flexuosa* and when there are no fruits on the ground). We found that 67.9% of seeds remained in faeces, 28.9% were removed, and 3.2% were depredated *in situ*. Rodents removed more seeds under shrub cover than on bare soil, and during the non-fruiting period than during the fruiting period, whereas ants removed similar proportions of seeds in different microhabitats but almost exclusively during the fruiting season. This work acknowledges the complexity of dispersal processes and identifies the relative importance of some environmental factors for seed fate.

Zusammenfassung

Das Schicksal von aus Säugetierkot verbrachten Samen ist abhängig von der Art des Tieres, das die Samen findet und von den Umgebungsbedingungen. In den lichten *Prosopis flexuosa*-Wäldern der zentralen Monte-Wüste Argentiniens wurden der Samenfraß und die Samenentfernung aus dem Kot durch verschiedene Tiere sowie der Einfluss von Mikrohabitat und Nahrungsverfügbarkeit auf die Samenentfernung untersucht. In Ausschlussversuchen mit simuliertem Rinderkot quantifizierten wir die Samenprädation *in situ* (innerhalb von Käfigen) und die Samenentfernung aus dem Kot durch Nagetiere und Ameisen in zwei unterschiedlichen Mikrohabitaten (unter Sträuchern und auf nackter Erde) sowie bei unterschiedlicher Verfügbarkeit von *P. flexuosa*-Früchten (während des Fruchtens und zu einer Jahreszeit als keine Früchte mehr zur Verfügung standen). Wir fanden, dass 67.5% der Samen im Kot verblieben, 28.9% aus ihm entfernt wurden und 3.2% *in situ* gefressen wurden. Nagetiere entfernten mehr Samen aus dem Kot, der sich unter Sträuchern befand und in der Zeit nach dem Fruchten von *P. flexuosa*,

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wohingegen Ameisen in beiden Mikrohabitaten etwa gleich viele Samen entfernten, dies aber fast ausschließlich während des Fruchtens von *P. flexuosa*. Diese Untersuchung verdeutlicht die Komplexität der Ausbreitungsprozesse und die Bedeutung von Umwelteinflüssen auf das Schicksal von Samen.

Introduction

Seed dispersal can be a complex multi-stage process (Vander Wall & Longland 2004, 2005; Vander Wall, Forget, Lambert, & Hulme 2005; Vander Wall, Khun, & Beck 2005) where the initial dispersal movement is usually obvious (*e.g.* wind, frugivorous animals), but subsequent movements are often not so evident. The potential fate of seeds deposited in faeces is immediate germination, dormancy, mixing into the litter by the action of trampling and faeces decomposition (Malo & Suárez 1995a, 1995b; Dai 2000; Campos, Mangeaud, Borghi, de los Rios, & Giannoni 2011), or removal by animals (Brown & Heske 1990; Price & Joyner 1997; Hulme & Benkman 2002). In arid and semiarid ecosystems, faecal material can be an unfavourable environment for seed survival and seedling establishment for three reasons. First, faeces can be exposed to harsh environmental conditions, such as extreme temperatures and radiation, which produce seed desiccation (Borchert & Tyler 2010). Second, seed aggregation in faeces may attract seed predators (Janzen 1982; Chapman 1989; LoGiudice & Ostfeld 2002). Third, if germination occurs, seedling competition can be strong (*e.g.* Loiselle 1990). Survival of seeds in faeces and seedling establishment has been associated with a second movement away from the point of deposition after primary dispersal (Vander Wall, Khun, & Gworek 2005). Therefore, seed removal from faeces appears as a relevant stage in the seed dispersal process which is worth assessing to understand the dynamics of seedling establishment and plant recruitment.

Nearly all existing studies that address secondary movement of seeds from faeces come from temperate and tropical systems (Vander Wall, Khun, & Beck 2005; Vander Wall, Khun, & Gworek 2005; D'hondt, Bossuyt, Hoffmann, & Bonte 2008; Manzano, Azcárate, Peco, & Malo 2010 and references therein), while in dry ecosystems we know almost nothing about this process. Studies from the tropics point out that dung beetles, ants and rodents are the major secondary seed dispersers (Vander Wall, Khun, & Beck 2005). Rodents have been historically considered seed predators, but certain species with scatter-hoarding behaviour (Wenny 1999; Feer & Forget 2002; Giannoni et al. 2013) play roles as both predators and dispersers (Theimer 2005). Ants also play a dual role because, although they consume many seeds, they may also disperse some of them (in trails and refuse dumps), thus influencing seed-bank dynamics and promoting seedling establishment of some plant species in tropical forests (Levey & Byrne 1993; Passos & Oliveira 2002). In the Monte desert,

some studies have studied the removal of *Prosopis flexuosa* fruits from under the trees' cover by small rodents, but there is no information on removal of seeds from faeces. We know that the sigmodontine rodent *Graomys griseoflavus* transports an important number of propagules, but they are left mainly in larders and later depredated, whereas *Eligmodontia typus* scatter-hoards propagules and leaves intact seeds removed from the fruits (Giannoni et al. 2013). Both species move fruits and store seeds at short distances (200 cm; Campos, Giannoni, Taraborelli, & Borghi 2007). Regarding ants, eleven species have been recorded exploiting *P. flexuosa* fruits, most of them remove the mesocarp *in situ*, and only *Acromyrmex* and *Pheidole* species were capable of carrying fruit segments (Milesi & Lopez de Casenave 2004).

Abiotic factors and ecological interactions can affect the fate of seeds in faeces. Attraction to high density of seeds clumped in faeces (Traveset 1990; Hulme 1994) and granivore satiation (Janzen 1971) influence the choices of secondary seed removers. Additionally, abiotic characteristics of the sites where faeces are deposited, such as vegetation structure (Christianini & Galetti 2007) and local availability of alternative food (Bermejo, Traveset, & Wilson 1998; LoGiudice 2001), affect animal foraging and the probability of a second dispersal event of seeds from faeces.

P. flexuosa is a keystone tree species in the Monte desert. It produces abundant fruits that accumulate on the ground, representing a source of food for a wide variety of organisms. Cattle may transport, disperse, and redistribute a large number of *Prosopis* seeds. However, survival of seedlings in dung is virtually negligible (Campos et al. 2008, 2011), and therefore a second movement may represent another chance for seeds to survive. Our main goal is to investigate the fate of seeds in faeces and to identify the particular ecological conditions that promote a second movement of seeds. To achieve this goal, we evaluate the magnitude of seed predation and removal from faeces by rodents and ants. Moreover, we assess the simultaneous influence that different microhabitats and availability of *P. flexuosa* fruits have on seed removal and predation. Using a field experiment with simulated cattle faeces, we aimed at answering the following questions: (1) Do rodents and ants differentially remove and depredate seeds found in faeces? (2) Does the microhabitat where the faeces are deposited affect removal and predation of seeds? (3) Does availability of *P. flexuosa* fruits influence removal and predation of seeds found in faeces? Regarding the last two questions, we expect to find: (a) lower seed removal and *in situ* predation on seeds located in faeces lying on bare soil,

because in covered areas probability of removal and predation should increase, and (b) lower or no removal and predation on seeds from faeces when *P. flexuosa* fruits are abundant on the ground, because we hypothesize that animals prefer fresh fruits and seeds over seeds in faeces.

Materials and methods

Area and species

The Monte desert biome is the driest region in Argentina (Fernández & Busso 1997; Abraham et al. 2009), and encompasses more than 38 million ha (Roig-Juñent, Flores, Claver, Debandi, & Marvaldi 2001). The study was conducted in the Man and Biosphere Reserve of Ñacuñán (34°02′ S, 67°58′ W), located in the central portion of the Monte desert (Morello 1958). This reserve has been free from livestock since 1972. Mean annual temperature is 15.9 °C. Rainfall occurs primarily between October and March, with a mean annual value of 333.5 mm. The major plant community in this area is open woodland composed of *P. flexuosa* trees and, in lower proportion, *Geoffroea decorticans* trees, within a matrix of xerophytic shrubs (*Larrea divaricata*, *Capparis atamisquea*, *Condalia microphyla*, *Lycium* spp., among others) (Roig & Rossi 2001).

P. flexuosa is a key species in the Monte desert biome (Kingsolver, Johnson, Swier, & Teran 1977) due to its important role in the organization and functioning of the community (Mares, Enders, Kingsolver, Neff, & Simpson 1977; Álvarez, Villagra, Rossi, & Cesca 2009; Aschero & Vázquez 2009; Cesca, Villagra, Passera, & Álvarez 2012). This species creates microhabitats under its canopy, formed by islands of vegetation thus acting as a nurse plant (Rossi & Villagra 2003). Such islands of vegetation are interspersed with sparse or absent plant cover. *P. flexuosa* fruits are indehiscent pods that ripen around early summer (December–January). Once fruits fall to the ground, they do not last there more than six weeks because they are consumed *in situ* or removed by numerous species of invertebrates, mainly ants (Milesi & Lopez de Casenave 2004), and vertebrates such as small rodents (Campos, Ojeda, Monge, & Dacar 2001; Giannoni, Borghi, Dacar, & Campos 2005), foxes, Patagonian hares, wild boars, cattle (Campos & Ojeda 1997), armadillos, skunks, and rheas (Campos et al. 2014). Pods are highly nutritive, with a thin epicarp and a spongy mesocarp rich in carbohydrates (Karlin, Coirini, Catalán, & Zapata 1997). Seeds (24–40 mg and 5 mm long) are within a woody endocarp which provides physical protection, and have an impermeable coat that provides dormancy. All these structures must be broken for germination to occur (Catalán & Balzarini 1992) but they allow many seeds to pass relatively unharmed through the guts of native and exotic mammals (Campos & Ojeda 1997; Campos et al. 2008). The faeces of some of these native mammals (*e.g.* Patagonian hares and foxes), may contain similar numbers of seeds in 100 g of faecal material as do cattle faeces (S. Velez, unpubl. data). Because cow dung is abundant and easy to find and manipulate, we chose this type of faecal material for our experiments.

Experimental design

We assessed seed predation and removal from faeces by simulating faeces with seeds. These seeds were extracted from fruits collected directly from trees during the previous fruiting season. Simulated faeces were prepared with dung from captive cattle, collected in the season when these animals do not feed on *P. flexuosa* fruits (winter–spring). Dung was homogenized and reshaped into single piles of 12 cm × 10 cm × 8 cm (considered a faecal unit), each with 20 seeds without endocarp.

We replicated the experiments in two 10-ha plots. On each plot we selected 10 *P. flexuosa* trees located at least 25 m apart. Associated with each tree we placed four faecal units in two different microhabitats, and accessible for rodents and ants (Fig. 1). We ignored the influence of dung beetle species in seed removal for two reasons: first, local abundance and diversity of dung beetles species present in our study site are very low; second, old and dry dung used in our experiments does not represent an attractive bait for dung beetles (M. B. Maldonado, unpubl. data).

In order to identify which animal group removed and depredated seeds located in faeces, we used two types of enclosure cages: a closed type, made with 0.75 cm × 0.75 cm wire-screen, sized 50 cm × 50 cm × 10 cm, which allowed access only to ants (Fig. 1); and an open type with similar dimensions and wire, but with four 4 cm × 6 cm openings on each side (Fig. 1), which allowed access to sigmodontine rodents and ants, but prevented the entrance of medium-size mammals and large seed-eating birds (Blendinger 2000). In order to assess the effect of microhabitat on seed removal and predation, we placed two cages on bare soil (one closed and one open cage) and two under shrub cover (one closed and one open cage) (Fig. 1). To assess how availability of *P. flexuosa* fruits affects seed removal and predation, we conducted the same experiment twice, using the same plots and trees: the first experiment was during the fruiting season for *P. flexuosa* (19 December–19 January, southern hemisphere summer), when abundant fruit can be found on the ground beneath the trees, and the second when no fruits are available on the ground (24 April–24 May, autumn). This design with contrasting fruit abundances at two points in time allowed us to effectively control availability of *Prosopis* fruits to animals. However, we acknowledge the limitation that other food types may be more abundant during autumn, which cannot be discriminated with this design.

We recorded seed removal and *in situ* seed predation per faecal unit after 30 days. Experiments followed guidelines used by other studies (*e.g.* Lopez de Casenave, Cueto, & Marone 1998; Giannoni, Dacar, Taraborelli, & Borghi 2001; Sassi, Tort, & Borghi 2004) that were based on the assumption
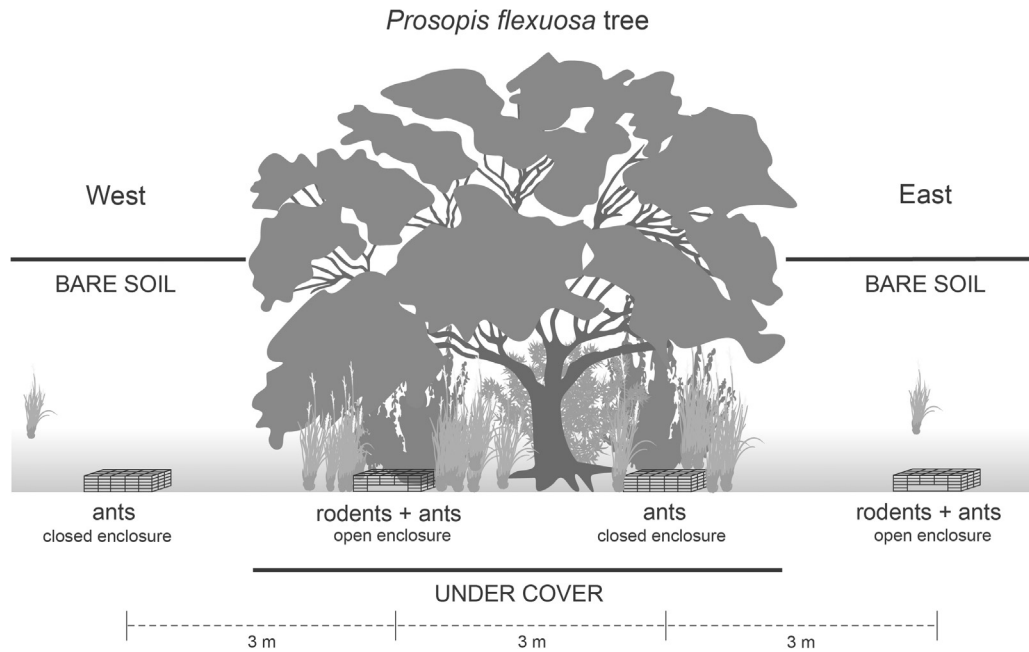
Fig. 1. Schematic representation of the experimental design. Each experimental unit associated with a *P. flexuosa* tree consisted of four enclosure cages placed at 3 m intervals: two cages on bare soil (one open and one closed) and two under shrub cover (one open and one closed).

that all seeds had similar probability of being found by animals. Seed removal per faecal unit was estimated as the number of offered seeds (20 in all cases) minus the number of depredated and remaining seeds. In order to estimate the number of seeds removed by rodents, we subtracted from the total number of seeds removed, the number of seeds removed by ants from the closed cage adjacent to the open cage (where both rodents and ants had access) located in the same microhabitat. *In situ* seed predation per faecal unit was estimated by counting seed parts around the remainder of the faecal unit within cages. Totally empty seed coats were assigned to predation by rodents (Villagra, Marone, & Cony 2002), and closed seed coats with traces of endosperm were assigned to predation by ants (some even had tiny ants inside) (Milesi & Lopez de Casenave 2004; S. Velez, unpubl. data).

Statistical analysis

To assess whether seed removal from faeces differs between both groups of animals, between microhabitats and under different fruit availability conditions, we fit a generalized linear mixed model (GLMM). For model building and selection we followed guidelines of Bolker et al. (2009), using the "lme4" package in R (Bates, Maechler, Bolker, & Walker 2014). Because the response variable was a proportion (number of seeds removed/seed offered), we assumed a binomial error structure and used a logit link function (McCullagh & Nelder 1989). We specified sites and trees as random effects. The fixed effects considered were animal group (with two levels, rodent and ant), microhabitat (with two levels, under

cover and on bare soil), and availability of *P. flexuosa* fruits (with two levels, fruits and no fruits). We built a full model, which involved all random effects, all main fixed effects, and their interactions. To define the stochastic part of the model, we examined the relationship between total variance and the variance from each random effect and kept those that explained more variability. To select the fixed factors on the deterministic part of the model, we applied a backward stepwise elimination method to several models with different combinations of fixed effects. For model selection, we used Akaike Information Criterion (Akaike 1981) corrected for small sample size (AICc) (Sugiura 1978; Hurvich & Tsai 1991). Models were compared by ΔAICc values (difference between the lowest AICc value of the best of suitable models and AICc from each of the other candidate models, generally accepted ΔAICc < 2) and the AICc weight (the strength of evidence in favour of one model over the others) (Burnham & Anderson 2002). The best model will have a ΔAICc of zero and the highest value of AICc weight. We extracted the coefficients of the selected fixed effects using the invlogit function (Gelman & Hill 2007) from the "arm" package in R (Gelman & Su 2014) in order to interpret and graph the estimated values of the response variable. Estimated standard errors from the model were also transformed back and provided as upper and lower values around the mean (they are not symmetrical around the mean when back transformed) (for calculation details see Appendix A).

The data on seed predation *in situ* were naturally scarce and there were two treatments with no predation. Thus, these results are commented very briefly in the "Results" section; observed means and standard errors are available in Appendix

Table 1. Models comparison of fitted models for seed removal by different animals (AG), in different microhabitats (MH), and availability of fruits (FA). Animals were rodents and ants, microhabitat was the site from where seeds were removed (under shrub cover and bare soil), and availability of fruits referred to different phenological stages, during fruiting season (summer) and during non-fruiting season (autumn). Asterisk means interactions between main fixed effects. Models are ranked in accordance to model selection procedures based on Akaike Information Criterion corrected for small sample size (AICc). The number of parameters (K), Akaike Information Criterion corrected (AICc), the delta AICc (ΔAICc), Akaike weights (Wi), and the cumulative Akaike weights (Cum. wi) are given.

Model	K	AICc	ΔAICc	Wi	Cum. wi
M1 = AG + MH + FA + AG*MH + AG*FA	9	710.66	0.00	0.70	0.70
M0 = AG + MH + FA + AG*MH + AG*FA + AG*MH*FA	11	712.98	2.32	0.22	0.91
M3 = AG + MH + FA + AG*FA	8	714.82	4.16	0.09	1.00
M2 = AG + MH + FA + AG*MH	8	747.22	36.56	0.00	1.00

A. Since open cages allowed the entrance of both animal groups and, hence, ants had access to both cages per microhabitat, we calculated the proportion of seeds depredated by ants by dividing the total number of seeds eaten by ants in a microhabitat by the total number of available seeds in that microhabitat (40 seeds).

All statistical analyses and plots were performed using R 3.1.1 language and environment (R Development Core Team 2014).

Results

Most seeds offered in the experiment remained in faeces (67.9%), while 28.9% (n = 925) were removed and only 3.2% were depredated *in situ* (n = 102). Overall, the mean proportion of seeds removed was 0.29 (±0.03 SE) per faecal unit, but we found an effect of the microhabitat on seed removal by rodents and also an effect of fruit availability on seed removal by ants. We fit a set of four candidate models to evaluate seed removal by rodents and ants under different environmental conditions. The best model (the one with the lowest AICc) included the second-order interactions between animal group and microhabitat, between animal group and fruit availability, and all main effects (Table 1). According to parameter estimation of our generalized linear models, fruit availability and the second-order interactions had a significant effect on seed removal (Fig. 2). The difference between the proportions of seed removed by rodents from under shrub cover and from bare soil was 40% during the fruiting season, and 48% during non-fruiting period (Table 2 and Fig. 3). Seed removal by ants
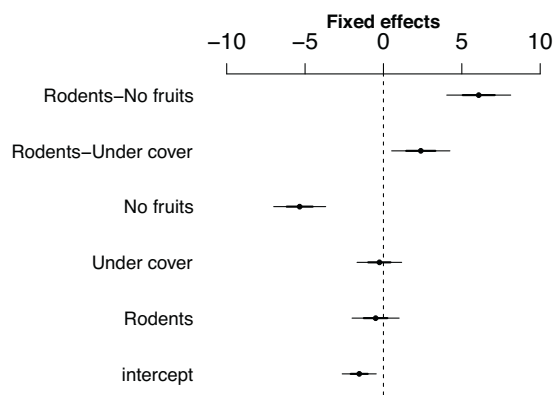

Fig. 2. Parameter estimation of selected model by generalized linear mixed model fit for testing the effects of animal group, microhabitat, and fruit availability on seed removal. Estimate of the means (dots) and standard errors (external line) were obtained from logit link function. Confidence intervals (inner line) were estimated from likelihood profiles.

occurred almost exclusively during the fruiting season (0.17 and 0.14 on bare soil and under cover, respectively), while during non-fruiting period it was notably scarce (less than 0.001 in both types of microhabitats) (Table 2 and Fig. 3).

The mean proportion of seeds depredated *in situ* was 0.02 (±0.006 SE) seeds per faecal unit. Seed predation by rodents under shrub cover, and during the non-fruiting period was higher than under the others treatment (0.06 ± 0.027 SE). We found no predation by rodents on seeds found on bare soil during the fruiting season, nor by ants on bare soil during the

Table 2. Proportion of seeds removed per faecal unit. Values are those estimated by generalized lineal mix models and transformed back means, superior, and inferior standard errors for seed removal by ants and rodents, in different microhabitats, and fruit availability.

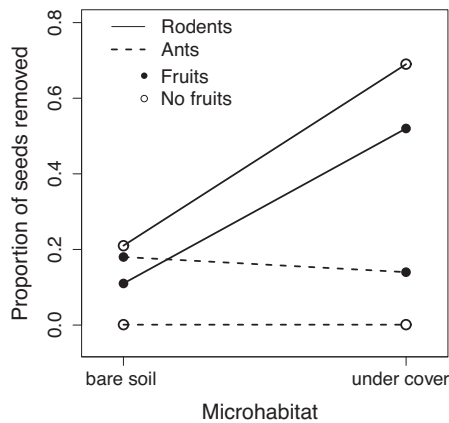| Fruit availability		Fruits				No fruits			
Microhabitat		Bare soil		Under cover		Bare soil		Under cover	
Animal group	Ants	0.18	+0.27 −0.11	0.14	+0.25 −0.07	0.001	+0.002 −0.0004	0.001	+0.002 −0.0003
	Rodents	0.12	+0.22 −0.06	0.52	+0.73 −0.30	0.21	+0.43 −0.09	0.69	+0.86 −0.28

Fig. 3. Predicted mean values (adjusted by a generalized linear mixed model and transformed back) of the proportion of seeds removed from faeces by rodents and ants, and second-order interactions between microhabitat and fruit availability. Fruit availability refers to the fruiting season in early summer (December–January) and non-fruiting period occurred during autumn (April–May). The fruiting season occurred in December–January (early summer) and no-fruits period occurred since April (autumn).

non-fruiting period (for *in situ* seed predation see Appendix A: Table 3).

Discussion

We evaluated key interactions during one stage of the dispersal process of *Prosopis*, and found that the probability of a seed being removed or depredated from faeces differs between predators, which in turn are affected differentially by type of microhabitat and availability of *P. flexuosa* fruits. Experiments assessing all these factors acting together can help us estimate the relative importance of environmental conditions for seed removal, and may allow us to identify and understand the ecological scenarios favouring seed survival. In *P. flexuosa* open forest of the central Monte desert, seeds in cattle faeces are removed mainly by small rodents under shrub cover and during the non-fruiting period. *In situ* seed predation is very low, and the highest proportion of seeds is depredated by rodents during the non-fruiting period.

One limitation of this study based on experimental estimations is the simplification of seed-animal interactions occurring in the study system, considering only cattle as *P. flexuosa* disperser (they certainly are not the only dispersers), and only rodents and ants as secondary seed dispersers. Dung beetles could have a role in seed removal between the first 48 h after dung deposition (fresh dung) but, due to their low abundance in the livestock-excluded sites, their role as seed removers may be less important (M. B. Maldonado, pers. comm.).

Cattle can transport huge amounts of *P. flexuosa* seeds and often many seeds can germinate in the field immediately after defecation; however, seedlings survive for a very short time

(Campos et al. 2011). Our results support previous studies showing that a second seed dispersal event has the potential for furthering seed movements, and probably offers different benefits to plants (Wang & Smith 2002; Vander Wall & Longland 2004, 2005).

In response to our first question, whether seed removal and predation differ between rodents and ants, we found that seed removal from faeces by rodents appears to be quantitatively more significant than removal by ants. Because of their larger body size and better manipulation capacity, rodent species of the Monte are capable of exploiting this resource faster than ants (C. Campos, unpubl. data) once they have found it (Giannoni et al. 2013). Rodents have been historically considered predators of seeds from faeces in most regions (Janzen 1982, 1986; Shepherd & Chapman 1998; Andresen 2002), even though seed removal by rodents does not necessarily entail seed predation because the fate of seeds depends on the foraging and food-storing behaviour of each rodent species. For instance, scatter-hoarding rodents may potentially disperse some seeds because they bury seeds in caches that they may not fully recover later (Forget & Milleron 1991; Vander Wall 2002; Vander Wall, Khun, & Beck 2005). While secondary dispersal by rodents has been well documented in the Neotropics (Andresen 2002; Feer & Forget 2002; Wehncke & Dalling 2005), and recently documented in a tropical montane forest in Africa (Nyiramana, Mendoza, Kaplin, & Forget 2011; Dutton, Chapman, & Moltchanova 2014), this behaviour has not been studied in deserts, which leaves a gap in the global knowledge of the seed dispersal cycle in these biomes. The four sigmodontine species present in our study area could have some negative effects on the dispersal of *P. flexuosa* seeds. Although these rodents consume seeds *in situ*, they also remove, transport, and store propagules in both larder- and scatter-hoarding patterns (Campos et al. 2007; Giannoni et al. 2013). However, the unprotected state of seeds (without hard endocarp) in cattle dung could represent a suitable condition for rodents to eat seeds with a minimum cost of searching and gnawing, promoting seed predation rather than storage.

Ants also remove, eat, transport and disperse seeds recovered from vertebrate faeces or regurgitations (Vander Wall, Khun, & Beck 2005; Vander Wall & Longland 2005). In our study site, at least eleven species of ants have been recorded interacting with *P. flexuosa* fruits: eight of them (*Camponotus punctatus*, *Crematogaster quadriformis*, *Forelius nigriventris*, *Forelius* sp., *Dorymyrmex* sp., *Pheidole* spp. and two species from unidentified genera) consume fruits *in situ*, while *Pheidole berghi* and two leaf-cutting ants (*Acromyrmex lobicornis* and *Acromyrmex striatus*) carry fruit segments and seeds to their nest (Milesi & Lopez de Casenave 2004). Leaf-cutting ants discard viable seeds in refuse dumps (S. Velez, unpubl. data) and could be playing a dual role as seed predators and dispersers. This special system that involves interactions between a non-myrmecochorous plant and non-harvesting ants is worth studying in more detail due to its implications for the secondary dispersal of *P. flexuosa*.

Since the influence of microhabitat on seed removal and predation, clearly affects seed removal by rodents, which occurs almost entirely under vegetation cover. This is consistent with other experiments at the same study site, which found that small mammals hoard seeds in microhabitats sheltered under shrubs (Giannoni et al. 2001; Taraborelli, Dacar, & Giannoni 2003; Taraborelli 2008). Small rodents inhabiting *P. flexuosa* open woodland prefer shrub, forb, and tree-covered microhabitats (Corbalán 2006; Corbalán, Tabeni, & Ojeda 2006). Searching, handling of faeces, and eating the seeds on bare soil could increase exposure of small mammals to predators. Predation risk can represent an important foraging cost to small desert rodents and may affect their foraging decisions (Hughes & Ward 1993). Our first prediction was not fully supported by the fact that seed removal by ants was unaffected by the microhabitat where the faecal units were located. The foraging areas preferred by ants depend on food type, food input, thermal conditions and inter-specific interactions as well as on species-specific traits like behaviour and social caste (Carroll & Janzen 1973; Traniello 1989; Delsinne, Roisin, & Leponce 2007). Therefore, the species composition of the ant assemblage at the study site, involving at least three species, likely with different foraging strategies and habitat preferences, may offset the levels of seed removal in different microhabitats. From the plant's point of view, seeds in faeces under shrubs have high probability of being moved and perhaps depredated by small rodents, and seeds in faeces located in open places still have a chance to be removed and probably dispersed by ants.

Food availability also drives the fate of seeds by affecting the behaviour of seed consumers (Forget 1993; Forget, Kitajima, & Foster 1999; Feer & Forget 2002). Some rodents avoid seeds in faeces in the presence of alternative food (Bermejo et al. 1998; LoGiudice 2001; Villagra et al. 2002); hence, post-dispersal seed predation or survival is strongly influenced by the availability of more palatable types of food, or more accessible food sources (LoGiudice & Ostfeld 2002). In desert ecosystems, where food resources are scarce and their availability is unpredictable (Costa 1995), seeds in faeces could represent an alternative food source that animals use in an opportunistic way when other, more satisfactory, food sources are absent (Bermejo et al. 1998; LoGiudice 2001; LoGiudice & Ostfeld 2002). We relied on those studies to formulate our second prediction about the exploitation of seeds in faeces in the absence of other food sources, but the prediction was not supported by our results. Even if rodents (contrary to ants) removed more seeds from faeces during the non-fruiting period, both animal groups removed seeds from faeces even in the presence of abundant fruits and other food available during the summer. We suggest that seeds in faeces do not represent a resource that animals use as an alternative food during scarcity of resources.

This study is the first to focus on removal and predation of seeds found in faeces in an arid environment away from the tropics, where this process has usually been studied. Two-step dispersal mechanisms (Vander Wall & Longland 2004, 2005) must be explored more deeply to understand the regeneration cycle of *P. flexuosa*, which could result from several movements of seeds involving different plant–animal interactions in a particular ecological context.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2015.09.002.

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