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Qualitative aspects of the effectiveness of Culpeo foxes (*Lycalopex culpaeus*) as dispersers of *Prosopis alba* (Fabaceae) in a Bolivian dry valley

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A B S T R A C T

Foxes disperse several plant species in arid and semi-arid environments, but their effectiveness as dispersal agents still remains unclear. In this study, we examined qualitative components of the effectiveness of *L. culpaeus* as a disperser of *P. alba* seeds in an inter-Andean dry valley of La Paz, Bolivia. Specifically, we determined seed deposition microhabitats, and the probabilities of germination, seed removal and seedling recruitment in these microhabitats. Additionally, we assessed the effect of gut-passage on *P. alba* germination. We collected 159 scats, which contained a total of 3402 endocarps fragments. Foxes dispersed seeds into two microhabitats: open areas and under woody vegetation, but more frequently in the former. The probability of germination did not differ between gut-passed and control seeds, but control seeds germinated faster than gut-passed ones. The likelihood of removal was greater for endocarps fragments in open microhabitats than under woody vegetation. Only a small percentage of the seeds in each microhabitat germinated, but none survived more than a week. We conclude that although the Culpeo fox can defecate intact *P. alba* seeds, it does not provide effective dispersal services.

1. Introduction

It is widely acknowledged that seed dispersal by vertebrates is a key ecological process that influences the structure and dynamics of plant communities (Howe and Miriti, 2004). By consuming fruits, frugivores can move seeds away from parent plants (Wang and Smith, 2002). This process typically increases seed survival and seedling establishment by reducing the effects of negative density-dependence (Comita et al., 2014) and by allowing seeds to reach suitable habitats for recruitment (Howe and Smallwood, 1982). Hence, seed deposition patterns determine the initial template for plant regeneration (Nathan and Muller-Landau, 2000; Wang and Smith, 2002; Howe and Miriti, 2004). However, depending on the effectiveness of the disperser (*sensu* Schupp, 1993), this template may or may not translate into the same spatial pattern of seedling recruitment, A frugivores' seed dispersal effectiveness (SDE) is determined by two components; a quantitative and a qualitative component. The quantitative component of the SDE refers to the number of seeds dispersed by the frugivore, while the qualitative one refers to the probability that a dispersed seed will become a new recruit (Schupp et al., 2017). For a frugivore to provide high quality dispersal services, gut passage should not have a negative effect on seed viability or germination (Traveset et al., 2007), and most seeds should be dispersed to.habitats with high probabilities of establishment (i.e., directed dispersal, Wenny, 2001). Consequently, a disperser is considered effective when the dispersal services it provides have positive demographic consequences on plant populations (Schupp, 1993; Schupp et al., 2010).

Carnivores, and particularly foxes, are known seed dispersers of many plant species in semi-arid ecosystems (Castro et al., 1994; Campos and Ojeda., 1997; Varela et al., 2008; Rosalino et al., 2010; Cares et al., 2013). Compared to passerine bids, they are considered long-distance dispersers (Jordano et al., 2007; González-Varo et al., 2013), however, there is still no consensus on how effective they are. For example, in Mediterranean Spain, Farris et al. (2017) showed that Sardinian foxes provide directed dispersal (i.e., they are effective dispersers) to *Juniperus phoenicea*. In contrast, red foxes are not effective dispersers of *Celtis australis*, as they destroy most of its seeds during gut passage (Rost et al., 2012). Contrasting results have also been obtained for New World plant species, with some authors suggesting that seeds consumed by foxes may be scarified during digestion (Bustamante et al., 1992; Castro et al., 1994; Silva et al., 2005), whereas others indicate that seed passage does not have an effect on germination (León-Lobos and Kalin-

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Arroyo, 1994; Morales-Paredes et al., 2015). Similarly, there is evidence that foxes are effective dispersers for some plant species (e.g., Silva et al., 2005) and not for others (e.g., Bustamante et al., 1992). Therefore, the effectiveness of foxes as seed dispersers remains uncertain and likely varies according to plant species and habitat.

Prosopis alba Griseb. (Mimosaceae) is a common tree in semiarid regions of South America, including Argentina, Uruguay, Paraguay, Peru, Chile and Bolivia (Burkart, 1976). Its fruits are indehiscent pods with a sweet spongy mesocarp and a hard, woody endocarp that encloses black-colored seeds (Burkart, 1976). Both domestic (i.e., cows, donkeys) and wild fauna (rodents, guanacos, and foxes) consume its fruits (Campos and Velez, 2015). In the inter-Andean dry valleys near La Paz (Bolivia), the Culpeo fox (*Lycalopex culpaeus*) regularly feeds on *P. alba* pods when they are available. In fact, *P. alba* is the most abundant plant item in its scats at our study site (Pacheco and Maldonado, unpublished data). Nonetheless, although the Culpeo fox disperses *P. alba* seeds (Maldonado et al., 2014), it is unknown whether it constitutes an effective disperser of this plant.

In this study, we assessed three features of the qualitative component of *P. alba* seed dispersal by the Culpeo fox. Specifically, we determined: 1) the habitats where *L. culpaeus* disperses *P. alba* seeds, 2) the effect of seed passage through the foxes' digestive tract on the frequency and temporal pattern of germination and, 3) the probability of seedling recruitment in the microhabitats where seeds are dispersed.

We hypothesized that if the Culpeo fox is an effective disperser *of P. alba*: 1) the microhabitats where it most frequently disperses seeds will have lower seed removal rates than those where seed dispersal is more infrequent, 2) the microhabitats where seeds are most frequently dispersed will have higher seedling recruitment probabilities than those where seed dispersal is less frequent and, 3) gut-passed seeds will have higher and faster germination rates than non-dispersed seeds.

2. Materials and methods

2.1. Study area

We conducted this study in two localities of an inter-Andean dry valley located south of La Paz, Bolivia: 1) Llacasa (16° 39′01.59″S, 68° 03′42.06″W, 3300–3600 m a.s.l.) and 2) "Club de Tenis La Paz" (16° 37′324″S, 68^{O}03′554″W, 3050–3080 m.a.s.l.). The latter is a private club that retains patches (~8 ha) of natural vegetation. The area has a mean annual temperature of 15.5 °C and receives on average 432.5 mm of rain (Beck and García, 1991; Miranda Torrez et al., 2015). At the study sites, *P. alba* trees have immature and ripe pods between December and February, and April and October, respectively (L. Pacheco, *unpublished data*).

2.2. Experimental design

We collected scats in Llacasa on four occasions between September and November of 2014; during two of these occasions we recorded the microhabitats where each scat was found and, based on what we observed, determined two microhabitats where scats were frequently deposited: 1) open areas (i.e., with no woody vegetation cover) and 2) under woody vegetation. To determine the relative frequency of scat deposition into each of these two microhabitats, we sampled six 2-m transects of different lengths (128 m, 158 m, 400 m, 400 m, 493 m, 671 m) at the Llacasa site and recorded the number of scats found in each microhabitat per transect. Transects differed in length due to the topography of the area. Collected scats were individually stored in paper bags and then manually fragmented in a laboratory to separate plant (i.e., fruits, seeds) from animal (i.e., bones, hair) material. *P. alba* fragments found in scats were classified as: 1) endocarps with relatively large quantities of mesocarp and exocarp remaining, 2) endocarps with little or no mesocarp remaining and, 3) bare seeds. Additionally, we tallied the number of *P. alba* seeds per scat.

To assess how passage through the Culpeo fox's digestive tract influences seed germination probabilities, we placed seeds from dispersed endocarp fragments (hereon gut-passed seeds) and seeds from pods collected under 20 trees (control group) in plastic Petri dishes lined with moist filter paper; we placed 10 seeds per dish and replicated each treatment 20 times. All Petri dishes were placed in an incubation chamber (Binder, Model BD-53) at 25 °C and germination was recorded periodically for up to 45 days.

We assessed the effect of microhabitat on post-dispersal seed predation by establishing banks of dispersed endocarp fragments in open areas and under woody vegetation. We left 20 banks per microhabitat, each containing 20 endocarp fragments. Banks were separated by at least 50 m from each other, corresponding to the average distance calculated between collected scats. We tallied the number of endocarp fragments removed at each bank after 48 h, 7, 30 and 60 days, and assumed that removed endocarps had been either predated, or removed by some secondary seed dispersers. Because not all removed endocarps are necessarily predated (i.e., removal may also result in secondary dispersal), this is a conservative estimation of seed predation rates, and this is likely an over estimation of seed predation rates as we assume predation of removed seeds.

We determined if the probability of seedling emergence differed between open habitats and under woody vegetation by sowing banks of 17 seeds from dispersed endocarps in each microhabitat replicate (N = 20/microhabitat). Each replicate was separated at least 50 m from each other and protected from rodent removal with 8 × 15 cm wicker enclosures. The experiment was set up between March and April of 2015 at Club de Tenis La Paz, and seedling emergence was monitored twice a week for 45 days and once a month for six months.

2.3. Data analysis

To determine if the frequency of scat deposition was similar between the two microhabitats where scats were found, we used a permutation-based chi-square test. We used Cox proportional hazards regressions (Lagakos, 1992; Fox, 2001) to compare: 1) the temporal pattern of germination between gut-passed and control seeds and, 2) removal rates between habitats. In this analysis, the dependent variable is a hazard function (1-expβ) that describes how the hazard (e.g. "risk" of emergence or seed removal) changes over time, and the effect parameter describes how this hazard relates to different seed treatments (control or gut-passed) or habitats. Additionally, we used GLMs with Poisson error distributions (link = "log") to compare the number of germinated gut-passed and control seeds and the number of removed endocarps in each habitat. All analyses were conducted using the R statistical environment (R Development Core Team, 2015; R Foundation for Statistical Computing, Vienna, AT).

3. Results

We collected a total of 159 scats and found that the Culpeo fox defecates more frequently in open areas than under woody vegetation ($\chi^2 = 12.65$, $P < 0.05$). Scats contained mammal hair and bones (likely from Rodentia and Lagomorpha), feathers (unidentified species) and seeds of three plant species. We found *Schinus arreira* seeds in 18.8% of the samples, and *Prunus persica* and *P. alba* endocarps in 1.9%, and 68.6% of the scats, respectively.

We found a total of 3402 *P. alba* endocarp fragments in the scats. On average, each scat had 21 (SD = 27.6) endocarp fragments; however, 33% of the scats contained no seeds and approximately 3% had more than 100. Only 11 of the 3402 endocarp fragments found were still attached to the mesocarp and exocarp. We did not find free seeds in the scats.

The number of germinated seeds did not differ between gut-passed (Mean = 0.54 seeds, SD = 0.21) and control seeds (Mean = 0.62 seeds, SD = 0.30) (Fig. 1) ($\chi 2 = 1.31$, df = 1, $P = 0.32$). However, the