

Frugivory and seed dispersal by foxes in relation to mammalian prey abundance in a semiarid thornscrub

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Abstract We examine the role of the native fox, *Pseudalopex culpaeus*, as a frugivore and seed disperser in a semiarid thornscrub of Chile. We quantified the fruit and animal components in its diet *versus* the availability of fruits and small mammals in the field over a 2-year period (January 1998 through February 2000). We tested the legitimacy and effectiveness of foxes as dispersers by quantifying the percentages of seed viability and of germination of seeds that passed through fox gut *versus* those picked from plants. We also studied their efficiency as dispersers, monitoring the fate of seeds in faeces placed in the field. The highest frequencies of fruit consumption by foxes were observed when abundances of small mammal prey were <6 individuals per hectare, regardless of fruit abundance in the field. Thus, foxes consumed fruits as a supplementary food resource. Based on 326 faeces, the total number of fruits consumed was about 34 000 over the 2-year study period, and fruits from the alien shrub *Schinus molle* represented 98% of that total, with the native *Portieria chilensis* a distant second. Germination and viability of defecated seeds of *P. chilensis* were reduced by 66% and 48%, respectively, in comparison to controls. In contrast, germination of seeds of *S. molle* increased by 50% and no effect on viability was observed. With regard to *P. chilensis*, foxes were legitimate (they defecated viable seeds), but ineffective (seeds in faeces had lower germination than those taken directly from parental plants and there was no seedling establishment in the field) and inefficient dispersers (seeds in faeces were deposited on microhabitats hostile to seed germination and seedling establishment). However, with regard to *S. molle*, foxes were legitimate, effective (seeds in faeces had higher germination than those taken directly from parental plants; there was germination but no establishment in the field), and efficient dispersers (over 41% of seeds were deposited on safe microsites). Thus, a native fox may be contributing to the spread of an alien shrub, co-opting existing community processes.

Key words: Chile, effectiveness, germination, legitimacy, *Pseudalopex culpaeus*, viability.

INTRODUCTION

The net result of frugivore activity is fruit removal, which may lead to successful seed dispersal if done by legitimate dispersers (Herrera *et al.* 1994). Whether fruit removal leads to successful seed dispersal depends largely on frugivore feeding behaviour, fruit processing, and postfeeding movements (Herrera 1989). Immediate influences on seed fate depend on whether seeds are damaged during mastication, regurgitation and digestion, and on whether seeds are dropped beneath the parent canopy or farther away (Debussche & Isenmann 1989, 1994; Jordano & Schupp 2000). Longer-term influences on seed and seedling survivorship depend on the type of microsites where seeds are deposited (Herrera 1998; Jordano & Schupp 2000). Studies of the plant-frugivore relationship have been approached from several perspectives. Some have focused on the passage of seeds through the gut (Malo & Suarez 1998), on the deposition of

seeds in safe microsites (Eriksson & Ehrlen 1992), on the dormancy of seeds (Izhaki & Safriel 1990), and on fruit traits such as seed/pulp ratios, taste and colour (Herrera 1989). In this context, it has been proposed that plant-frugivore interactions may influence the structure and function of plant communities (Izhaki *et al.* 1995; Malo & Suarez 1995, 1998). Although it is well-known that many carnivorous mammals commonly ingest fleshy fruits, their relevance as seeds dispersers has been little studied (Herrera 1989; Pigozzi 1992; Corlett 1998). Here we address the role of the culpeo fox *Pseudalopex culpaeus* as a frugivore and seed disperser in a semiarid thornscrub of Chile.

Throughout its range of distribution in Chile, the diet of *P. culpaeus* consists chiefly of rodents, but also includes lizards, birds and insects (Medel & Jaksic 1988). In addition, the presence of viable seeds has been documented in fox faeces, and it has been hypothesized that *Pseudalopex* foxes may be important seed dispersers (Armesto *et al.* 1987; Armesto & Rozzi 1989; Willson *et al.* 1995). Still, the role of these foxes as seed dispersers is open to discussion. Bustamante *et al.* (1992) found that culpeo foxes were legitimate

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Accepted for publication April 2005.

dispersers of the native shrub *Cryptocarya alba* (that is, they defecated viable seeds), that they were effective (seeds in faeces had higher germination rates than those taken directly from the parental plant), but that they were inefficient (because they deposited faeces in microsites hostile to seed germination and seedling establishment). On the other hand, Leon-Lobos and Kalin-Arroyo (1994) concluded that *Pseudalopex* sp. were legitimate, but less effective and clearly inefficient dispersers of seeds of the native shrub *Lithrea caustica*. Finally, Castro *et al.* (1994) concluded that culpeo foxes were legitimate, effective and efficient seed dispersers of the alien shrub *Schinus molle*.

Despite previous efforts to evaluate the relationship between *Pseudalopex* foxes and fruit plants, a systematic evaluation of food availability and phenology has not been carried out for an extended period. This information is crucial to interpret the specificity of the frugivore-plant relationship. Three attributes of frugivores should be evaluated in order to test their presumed favourable effects on plants. (i) Disperser legitimacy, which is the occurrence of apparently undamaged seeds in disperser faeces (Herrera 1989). (ii) Disperser efficiency, that is, their capacity to deliver seeds to safe sites, which is likely to result in survival and germination (Reid 1989). (iii) Disperser effectiveness, which is the proportion of recruited seedlings where a particular dispersal agent was responsible for their dissemination (Reid 1989).

Consequently, the objectives of this study were: (i) to document the relative importance of fruits in the diet of the culpeo fox as a function of the abundance of small mammal prey and fruit in the field; (ii) to test the legitimacy and effectiveness of this fox as a disperser, considering differences in seed viability and germination after passage through the fox gut; and (iii) to gauge the efficiency of culpeo foxes as dispersers, considering the fate of seeds in faeces deposited in the field.

METHODS

Study area

Las Chinchillas National Reserve, at Auco (31°30'S; 71°06'W), is a rugged area with elevations ranging from 400 to 1700 m, located in the Coastal Ranges, 300 km north of Santiago, Chile. The climate is defined as semiarid, with scarce rainfall concentrated in the winter months (di Castri & Hajek 1976). Mean annual precipitation is 175 mm but with high interannual variability (Jaksic *et al.* 1996). The vegetation is thorn-scrub, with species composition depending on solar exposure (Gajardo 1978; Jiménez *et al.* 1992). Slopes that face north (equatorial) receive higher solar radiation and have sandy soils with scattered gravel

patches and rock outcrops. Because of the more xeric character of these slopes, grasses are scarce (mainly *Nassella* spp. and *Stipa* spp.), but cacti (*Trichocereus* spp., *Tephrocactus ovatus*), bromeliads (*Puya berteroni-ana*) and sclerophyllous shrubs (*Bahia ambrosioides*, *Cordia decandra*, *Bridgesia incisaefolia*, *Flourensia thurifera*) are abundant. In contrast, slopes that face south (polar) receive less solar radiation and thus are more mesic. Soils appear to contain more organic matter, grasses are more abundant, there are no cacti or bromeliads, and a different assemblage of shrubs prevails (*Adesmia* sp., *Porlieria chilensis*, *Colliguaya odourifera*, *Proustia* sp.; Jiménez *et al.* 1992).

Small mammal abundance

Small mammal populations were monitored through mark-recapture procedures on two opposite-facing slopes of El Cobre creek. Trapping was performed monthly for five consecutive nights from January 1998 to February 2000 on two grids, each with a seven rows by seven columns configuration (= 49 traps per grid). Each trapping grid had trapping stations separated by 15 m, thus covering an area of 105 by 105 m (including a boundary strip of 7.5 m, or 1.1 ha). One grid was on an equatorial slope and the other on the opposite (polar) slope, separated at the base by about 50 m horizontal distance across a ravine. The grids contained one Sherman trap per station, with traps activated simultaneously on the equatorial and polar facing slopes. All traps were kept permanently in the field and closed when not in use. We baited traps with rolled oats during the evening, and checked them every morning. Each individual captured was marked with a metal ear tag and its body mass, sex and reproductive condition were determined. Density of each species was estimated as the minimum number of individuals known alive divided by 2.2 ha, at the end of each five-day trapping session. Jiménez *et al.* (1992) provide full details on trapping methods at the study site.

Fox life history

The culpeo fox (*P. culpaeus*) inhabits western South America from southern Colombia to Tierra del Fuego (Berta 1987). It is the second largest canid in South America, averaging 7 kg (Crespo 1975). The diet of this species (reviewed by Medel & Jaksic 1988) consists mainly of rodents, but also locally and seasonally includes lagomorphs, lizards, birds, insects and fruit. The culpeo fox is monoestrous (one litter per year) with a reproductive period between mid-August to the beginning of December. The principal time of birth is from October to December, with 3–5 pups per litter (Crespo 1975).

Fox diet

We analysed fox faeces collected monthly from January 1998 to February 2000. Faeces were collected at El Cobre creek along a fixed 3-km transect in the ravine that separated the two slopes with trapping grids. Faeces were also picked up when encountered in the trapping grids. We recorded location and date for each faecal sample, and are confident that they were from foxes, the only canids at the study site. We dried faeces and separated the major components. The number of individual prey items was estimated on the basis of paired or unique anatomical elements such as crania, mandibles, teeth rows, wings, elytra, fruits and seeds. We identified animal items to the finest resolution feasible (species for vertebrates, families for invertebrates), but grouped them by broader categories for subsequent analysis.

Biomass of mammal species at the study site was obtained from Jaksic *et al.* (1996). Unidentified cricetids and unidentified rodents (either cricetid or caviomorph), were assigned the arithmetic mean mass of the different cricetids or rodents identified in the diet. For other vertebrate prey in the diet (avian, reptilian and amphibian) we assigned, based on field experience, the following mean masses: 20, 80 and 5 g, respectively. For invertebrates (mainly arthropods), we arbitrarily assigned – and likely overestimated – a mean mass of 1 g. Seeds were identified to species, and we later estimated the number of fruits consumed by using the mean number of seeds counted in fruits collected from parent plants. Indeed, each of the fruits consumed by foxes contained only one seed, except for the cactus *Trichocereus* sp., which bears 1000–1500 seeds per fruit. Based on field measurements of fruits, we estimated a mean mass of 0.5 g. Monthly results were pooled by seasons as follows: autumn (March–May), winter (June–August), spring (September–November) and summer (December–February).

Fruit abundance

Fruit abundance in the field was assessed for the two species with the highest counts in fox faeces. *Schinus molle* (Anacardiaceae), a species introduced from Peru to Chile since Inca times, has red fruits that measure 4–6 mm in diameter and contain a single seed that measures 3–5 mm in diameter. *Porlieria chilensis* (Zygophyllaceae) is a species endemic to Chile; its fruit is a violet-coloured capsule when ripe, and which contains a single seed that measures 8–10 mm (Rodriguez *et al.* 1983). For the shrub *S. molle*, 30 individuals around the Reserve's administrative headquarters were tagged and monitored. For the shrub *P. chilensis*, 20 individuals at El Cobre creek and 10 at

El Grillo creek (2 km away from El Cobre creek) were tagged and monitored. Six sampling quadrats, 50 by 50 cm, were fixed to each individual shrub at a height > 1.2 m above the ground (beyond the reach of foxes). All fruits inside such quadrats were counted. Abundance of these fruits was measured during May 1998, July 1998, September 1998 to February 1999, April 1999, July 1999, September to October 1999, December 1999, January 2000 and March 2000. These results were pooled by season, as defined above.

Seed germination, viability tests and seed dispersal

Viability and germination of seeds were determined in the laboratory, to find out whether passage through fox gut affected seeds. We carried out a study of viability and germination of seeds of *Schinus molle* and of *Porlieria chilensis* obtained directly from parental plants in comparison to seeds in fox faeces collected in September 1998. All seeds in 40 faeces were pooled and five samples of 50 seeds each per plant species were randomly chosen for germination trials. Simultaneously, five samples of 50 control seeds were picked up directly from the two plant species. All seeds were set to germinate in Petri dishes containing saturated filter paper. Humidity (60–70%), temperature (25°C), and photoperiod (L:D, 12:12) were maintained constant. We considered that a seed germinated if a radicle of at least 5-mm length was observed within an 80-day period, after which percent germination was calculated. Viability tests were carried out on seeds obtained from the same 40 faeces collected in September 1998. In the case of *S. molle*, eight samples of 40 seeds each were taken, and in the case of *P. chilensis*, four samples of 50 seeds. As controls, eight samples of 40 seeds and four samples of 50 seeds were obtained directly from the respective parental plants. All seeds were cut in half first, kept in water for 24 h and immersed in TTC (Tripheniltetrazolium; see Barton 1961; Grabe 1970), and kept in the dark. After a further period of 24 h, seeds with a wholly or partially coloured embryo were considered viable.

We also checked seed dispersal, germination, establishment and seedling abundance of *S. molle* and *P. chilensis* in the field. We recorded the number and species of seeds in each faeces, and the site where each faeces was found. *A priori*, we classified microhabitats as either favourable (e.g. bottom of ravines, wet microsites) or unfavourable for germination (e.g. open sites, dry microsites). Dispersed seeds in faeces were assigned to either of these categories and monitored quarterly from July 2000 to October 2003.

In addition, 11 faeces containing seeds were left whole, marked and either placed in the open ($n = 5$ in unfavourable microhabitat, 400–600 m apart, along a 3 km transect) or under the canopy of shrubs ($n = 6$

in favourable microhabitat, 400–600 m apart, along a 3-km transect) in June 1998, and monitored every month until March 2000 to determine germination and seedling establishment.

Statistical analyses

To test whether passage through fox gut affected seed germination and viability, the percentage germination was arcsine-transformed prior to ANOVA testing (Sokal & Rohlf 1981). Data were analysed using the Statistica (StatSoft 1997) statistical package for Windows 95.

RESULTS

Fruit and mammal consumption

A total of 326 faeces was analysed, of which 103 (32%) contained seeds. Throughout the 2-year study period, vertebrates and invertebrates constituted the staple prey of foxes, and vertebrates contributed the most biomass. There were 532 individual animal prey items identified (19 218 g), of which small mammals represented 56% by number (17 940 g = 93% by mass), other vertebrates 10% (1100 g; 6%), and invertebrates 34% (178 g; 1%; Table 1). About 34 000 fruits were consumed, based on the number of seeds counted (17 267 g), *Schinus molle* representing 98% and all other species the remaining 2%. Fruit consumption was not homogeneous throughout the year; it was observed only during four of the nine seasons

encompassed by our study (Table 1). Interestingly, the main fruit item was permanently available in the field: abundance of *S. molle* fruits fluctuated from 267 to 669 m⁻² of shrub canopy throughout the study, with no clear seasonal patterns but with some interannual variability (Fig. 1). In contrast, fruits of *P. chilensis* were present only during spring and summer, at an order of magnitude below the abundance of *S. molle* (from 0.0 to 30.6 m⁻²).

The highest consumption of fruits by foxes occurred when fruits were at their lowest abundance (Fig. 1). The temporal course of fruit consumption and small mammal abundance shows that the number of fruits ingested by foxes was higher when the abundance of small mammals was lower (Fig. 2). The highest values of fruit consumption were observed when the abundances of small mammals were ≤6 individuals per hectare. When the abundance of small mammals was >6 individuals per hectare, foxes did not consume fruits at all (Fig. 3). When we evaluated mammal consumption by foxes as a function of fruit abundance in the field, no effect was apparent (Fig. 4).

Seed germination, viability and dispersal

Seeds of *S. molle* ingested by foxes had a significantly higher percentage of germination (by 50%) than those collected directly from plants (ANOVA; Table 2). However, no effect of gut passage on viability was found (ANOVA; Table 2). In contrast, seeds of *P. chilensis* showed significantly lower germination and lower viability after passing through the fox gut. Germination

Table 1. Diet composition, by number and by biomass, of culpeo foxes (*Pseudalopex culpaeus*) in semiarid Chile. Number of fruits estimated from number of seeds in faeces

Food items	Summer 1998	Autumn 1998	Winter 1998	Spring 1998	Summer 1999	Autumn 1999	Winter 1999	Spring 1999	Summer 2000
<i>Schinus molle</i> fruits	0	0	0	0	1811	19 127	12 240	0	584
<i>Schinus polygamus</i> fruits	0	0	0	0	180	435	5	0	0
<i>Porlieria chilensis</i> fruits	0	0	0	0	0	7	0	0	2
<i>Prosopis</i> sp. fruits	0	0	0	0	0	23	0	0	0
<i>Atutemus</i> sp. fruits	0	0	0	0	0	1	0	0	0
<i>Trichocereus</i> fruits	0	0	0	0	2	3	0	0	10
Unidentified fruits	0	0	0	0	0	0	0	0	105
Total no. fruits	0	0	0	0	1993	19 596	12 245	0	701
Total g fruits	0	0	0	0	996.5	9 798	6 122.5	0	350.5
Total no. mammals	35	34	43	46	59	43	23	7	9
Total g mammals	2100	2040	2580	2760	3540	2 580	1 380	420	540
Total no. other vertebrates	5	6	2	14	9	8	2	3	6
Total g other vertebrates	100	120	40	280	180	160	40	60	120
Total no. invertebrates	25	0	42	3	45	28	11	12	12
Total g invertebrates	25	0	42	3	45	28	11	12	12
Total no. animal prey	65	40	87	63	113	79	36	22	27
Total g animal prey	2225	2160	2662	3043	3765	2 768	1 431	492	672
Total no. faeces	31	35	36	40	55	67	35	8	19

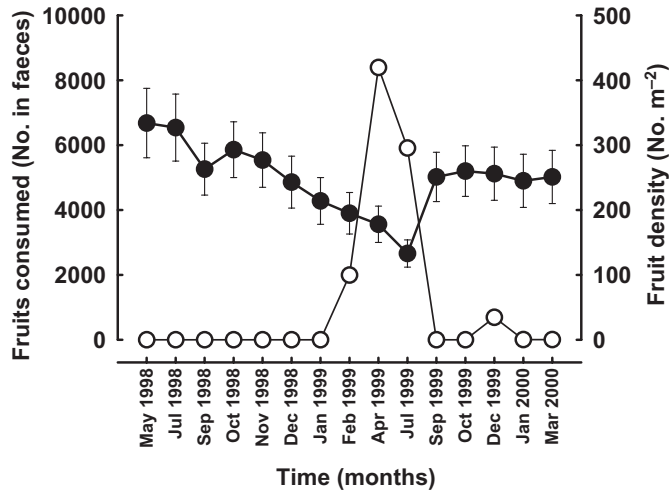


Fig. 1. Fruit consumption by culpeo foxes in comparison to field density of *Schinus molle* and *Porlieria chilensis* fruits (summed), in semi-arid Chile, 1998–2000. Values are mean \pm SE. (○) Fruits consumed (No. in faeces), (●) fruit density (No. m^{-2}).

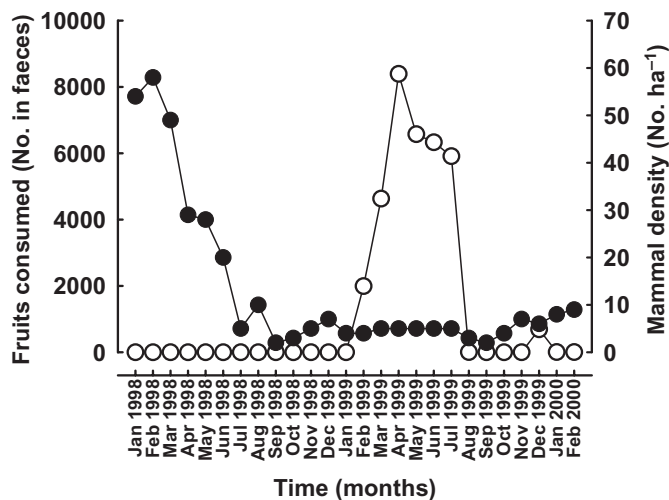


Fig. 2. Monthly fruit consumption by culpeo foxes in comparison to monthly small mammal density, in semi-arid Chile, 1998–2000. (○) Fruits consumed (No. in faeces), (●) mammal density (No. ha^{-1}).

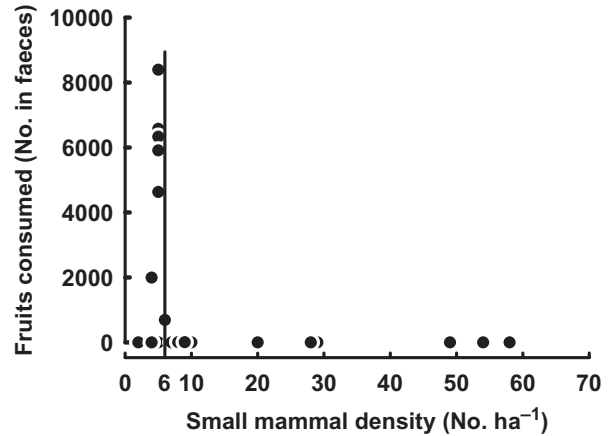


Fig. 3. Relationship between fruit consumption by culpeo foxes and density of small mammals in semi-arid Chile. Note threshold at mammal density ≤ 6 individuals per hectare (solid vertical line).

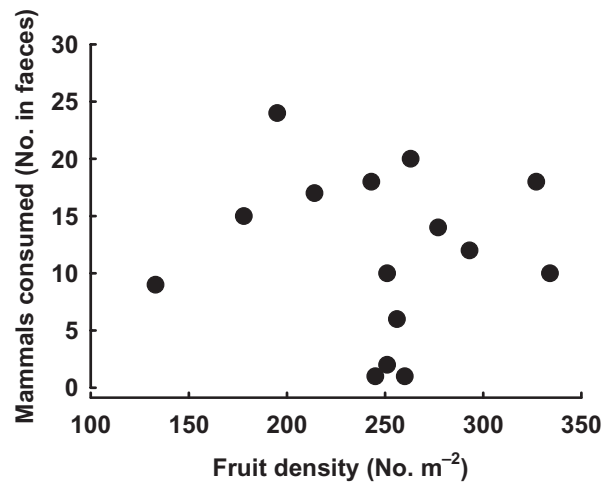


Fig. 4. Relationship between mammal consumption by culpeo foxes and field density of *Schinus molle* and *Porlieria chilensis* fruits (summed), in semi-arid Chile. Note lack of significant correlation ($r = -0.07$; $P = 0.78$).

Table 2. Percent viability and germination of seeds obtained from faeces of culpeo foxes and from parental shrubs in semi-arid Chile. Values are mean \pm SE (n)

Shrub seeds	Response	From faeces	From shrubs	ANOVA
<i>Schinus molle</i>	Germination	76.8 \pm 10.2 (250)	51.2 \pm 7.7 (250)	$F = 20.17$; d.f. = 1,8; $P = 0.002$
	Viability	95.9 \pm 5.2 (320)	95.6 \pm 4.6 (320)	$F = 0.016$; d.f. = 1,14; $P = 0.89$
<i>Porlieria chilensis</i>	Germination	42.8 \pm 2.9 (250)	64.8 \pm 6.7 (250)	$F = 13.25$; d.f. = 1,8; $P = 0.006$
	Viability	35.5 \pm 3.3 (200)	74.5 \pm 3.2 (200)	$F = 96.06$; d.f. = 1,6; $P < 0.005$

decreased from 64.8 to 42.8% and viability from 74.5 to 35.5% (ANOVA; Table 2).

We surveyed for naturally occurring shrub seedlings of *S. molle* and *P. chilensis* in the eight main ravines at the study site (El Cobre, El Grillo, Agua de la Falda, Torca, Agua Dulce, Las Gredas, Las Moyacas and El Cuyano) as well as at El Tinte, which borders the Reserve. We failed to detect seedlings of *P. chilensis*, but in three ravines we did observe seedlings of *S. molle*: 7 in El Tinte, 12 in Las Gredas and 8 in Las Moyacas. The distance between these seedlings and the source patch at the Reserve headquarters (where the *S. molle* plantation is located) ranged from 3 to 6 km. Except for culpeo foxes (Silva 2001), no other dispersal agents are known for *S. molle* at the study site (Hoffman & Armesto 1994).

We found 432 fox faeces in the nine ravines, of which 158 (37%) contained seeds. The total number of fruits consumed, based on the number of seeds, was 30 220 for *S. molle*. Of the dispersed seeds, 12 488 (41%) were defecated in favourable microsites and the remainder (59%) in unfavourable ones. We detected spontaneous germination of 26 (0.2%) out of those seeds in favourable microsites, but none of them reached the stage of seedling by the end of our study.

DISCUSSION

Foxes consumed fruit chiefly during 1999, when mammal density was ≤ 6 individuals per hectare. As small mammal populations declined toward autumn and winter, fruit consumption increased. While small mammal populations increased toward spring 1999 and summer 2000, fruit consumption was nil, despite it being available. Null consumption of fruits was also observed during 1998, when small mammal abundance was high. On the other hand, mammal consumption did not depend on fruit abundance. This enables us to suggest that foxes consume fruits as a supplementary food resource, only when the availability of their main prey falls to levels ≤ 6 individuals per hectare in our study site.

Despite the abundance of other fruit types in Aucó (*Schinus polygamus*, *Colliguaya odorifera*, *Senna cumingii*) foxes fed almost exclusively on *Schinus molle* and rarely on *Porlieria chilensis*. The canopy cover of *S. molle* at the site is 0.05%, and that of *P. chilensis* is 0.25%. But while the latter is distributed throughout the study site, the former is found only in an isolated patch of 2 ha at the Reserve's administrative headquarters. Foxes may cue in on fruits of *S. molle* because it is a spatially concentrated resource and/or because they are particularly rich in lipids (Castro *et al.* 1994). Apparently *S. molle* is not consumed to meet the foxes' water requirements, as suggested for other fox species living in semiarid systems (Ball & Golightly 1992). In

fact, the water content of *S. molle* fruits is only 12.6% by weight (Silva 2001), and there are several permanent ponds in the study area, readily accessible to foxes.

Our results indicate that culpeo foxes do not damage seeds of *S. molle* by mastication, that they defecate live seeds, and that they do not affect the survival probabilities of those seeds. In addition, foxes at the study site travel daily distances that fluctuate 6–8 km (Jiménez 1993; see also Salvatori *et al.* 1999), carry a high number of seeds (400–600 per faecal pellet), and have a mean retention time of fruits in the gut ranging 12–18 h (Silva 2001). These are important factors for assessing the role of foxes as seed dispersers (Herrera 1989; Castro *et al.* 1994; Bustamante & Canals 1995). Interestingly, germination of fox-defecated seeds of *S. molle* was significantly higher than that of seeds extracted from parental plants. This increase in germination may be explained by chemical and physical scarification by the digestive enzymes or by washing away of the seed coat (mesocarp; Agrios 1991). These processes may result in the relaxation of dormancy imposed by the mesocarp, due to water incorporation, exchange of gases, or release of inhibitors in the testa teguments (Bewley & Black 1982). On the other hand, we observed a negative effect of fox consumption and digestive treatment on the germination and viability of *P. chilensis* seeds.

The effects of endozoochory on the viability and germination of seeds may play a key role in plant dynamics (Valido & Nogales 1994; Izhaki *et al.* 1995; Malo & Suarez 1995), but before reaching conclusions it is important to consider what takes place after dispersal. We observed that foxes displayed a dietary shift toward fruits when mammalian prey abundance reached a threshold ≤ 6 individuals per hectare. Once foxes became more frugivorous, they strongly preferred some (*S. molle*) and neglected other fruits (*P. chilensis*). Using the terminology of Herrera (1989) and Reid (1989), culpeo foxes were legitimate (they defecated viable seeds), but ineffective (seeds in faeces had lower germination than those taken directly from parental plants and there was no seedling establishment in the field) and inefficient dispersers (seeds in faeces were deposited on microhabitats hostile to seed germination and seedling establishment), with reference to the native shrub *P. chilensis*. However, with regard to the alien shrub *S. molle*, foxes were legitimate, effective (seeds in faeces had higher germination than those taken directly from parental plants; there was germination but no establishment in the field), and efficient dispersers (over 41% of seeds were deposited on safe microsites). Thus, a native fox may be contributing to the spread of an alien shrub, co-opting existing community processes.

Nevertheless, the degree of effectiveness of culpeo foxes in terms of seedling establishment is unclear.

This is because there are temporal and spatial fluctuations of environmental factors (precipitation, temperature, soil humidity, herbivory) that could affect establishment. For instance, in many dry regions, shrub and tree establishment occurs only during years with high rainfall. Perhaps foxes are more efficient agents during wet than during dry years. This possibility could be explored when the next El Niño event brings increased rainfall to the study site (Holmgren *et al.* 2001; Jaksic 2001).

ACKNOWLEDGEMENTS

Silva acknowledges a PhD fellowship from CONICYT-Chile. We thank Chile's Corporación Nacional Forestal (CONAF), specifically CONAF-IV Region, for allowing us to work at the Reserve and for providing logistic support. We are also grateful to Servicio Agrícola y Ganadero (SAG) for issuing permits to trap animals. We thank B. Saavedra for field assistance and E. Silva for laboratory and computer assistance. This research was supported by grant FONDECYT 298-0022 to S. I. Silva, by a grant from the Andrew W. Mellon Foundation to F. M. Jaksic and by grant FONDECYT-FONDAP 1501-0001 to the Center for Advanced Studies in Ecology & Biodiversity.

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