

## Are foxes legitimate and efficient seed dispersers? A field test

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### Abstract

Carnivorous mammals are presumed to be legitimate seed dispersers because they consume and defecate undamaged seeds. However, their efficiency has never been evaluated under field conditions. If carnivores are efficient, seeds must be deposited in "safe sites" to assure germination. We tested the legitimacy and efficiency of foxes as seed dispersers by evaluating germination of *Cryptocarya alba* seeds dispersed by *Dusicyon culpaeus*. Laboratory tests showed that defecated seeds are viable and germinate at higher proportion than controls. In the field, germination varied with habitat. Germination was greater for seeds located beneath shrub canopies whether or not seeds had passed through the digestive tract of a fox. Foxes deposited seeds more often in unprotected habitats than under shrubs. Therefore, foxes are legitimate but inefficient seed dispersers. Our evidence does not support the general hypothesis that dispersal is favorable for plants.

**Keywords:** Chilean matorral, dispersers, disturbance, efficiency, foxes, legitimacy.

### Résumé

Les mammifères carnivores sont supposés être de réels disséminateurs de graines, car ils consomment et défèquent des graines non endommagées. Néanmoins, leur efficacité n'a jamais été évaluée sur le terrain. Si les carnivores sont efficaces, les graines doivent être déposées dans des « lieux sûrs » pour assurer la germination. Nous avons testé l'efficacité de renards en tant que disséminateurs en évaluant la germination de graines de *Cryptocarya alba* dispersées par *Dusicyon culpaeus*. Les tests de laboratoire montrent que les graines déféquées sont viables et germent dans des proportions plus élevées que dans les témoins. Sur le terrain, la germination varie selon l'habitat. Elle est plus élevée pour les graines situées sous le couvert des arbustes, que les graines soient ou non passées par l'appareil digestif d'un renard. Les renards déposent plus souvent les graines dans des habitats non protégés que sous des arbustes. En conséquence, les renards sont bien des disséminateurs de graines, mais inefficaces. Notre travail va à l'encontre de l'hypothèse générale selon laquelle la dispersion est favorable aux plantes.

## INTRODUCTION

Seed dispersal is assumed to be advantageous for plants because dispersed offsprings may have an increased survival probability, by escaping from predators and by reaching particular microsites and/or recently opened patches following

disturbance (HOWE & SMALLWOOD, 1982; CLARK & CLARK, 1984; DIRZO & DOMÍNGUEZ, 1986). In this context, dispersal agents, e.g. frugivores, are mutualistic, as they increase parent fitness and recruitment processes (VAN DER PIJL, 1982; JANZEN, 1983). Three attributes of frugivores should be evaluated in order to test their presumed favorable effects on plants: (i) *disperser legitimacy*, that is, the occurrence of apparently undamaged seeds in their feces (HERRERA, 1989), (ii) *disperser efficiency*, that is, their capacity to deliver seeds to *safe sites*, which is highly likely to result in survival and germination (REID, 1989) and (iii) *disperser effectiveness*, that is, the proportion of recruited seedlings in which a particular dispersal agent was responsible for dissemination (REID, 1989). Recent studies suggest that carnivorous mammals are common consumers of fruits in mediterranean plant assemblages (JAKSIĆ *et al.*, 1980; ARMESTO *et al.*, 1987; HERRERA, 1987, 1989). It is assumed that they are legitimate disperser (HERRERA, 1989), although there have been no attempts to test this legitimacy. On the other hand, efficiency and effectiveness of mediterranean carnivores also remain to be evaluated. The dispersal of *Cryptocarya alba* seeds by *Ducisyon culpaeus* is an appropriate case study. In central Chile, a region of mediterranean climate, *D. culpaeus* foxes consume fruits of the evergreen tree *C. alba*, a common late-successional species of the mesic zones of the matorral (ARMESTO & PICKETT, 1985). *Cryptocarya alba* fruits are small (1-2 cm), red, fleshy drupes with one seed per fruit. Usually, *D. culpaeus* is considered an important seed disperser because it consumes large quantities of fruits all year-round and travels long distances (JAKSIĆ *et al.*, 1980; ARMESTO *et al.*, 1987). In this paper we test the legitimacy and efficiency of *Ducisyon culpaeus* as seed disperser. In order to do it, we compare the proportion of germination in fox-defecated seeds versus control seeds. Next, we describe *C. alba* seed-defecation pattern by foxes over different habitats, and compare seed germination and predation in different habitats. Additionally, we measure seed- and seedling abundance over these different habitats.

## METHODS

### Study sites

This study was carried out from May 1988 to September 1989 in shrubland areas of El Pangue, central Chile (Coastal Range, 33°17'S, 71°11'W). We recognized two qualitatively distinct habitat types: (i) "open" sites, with sparse shrubs dominated by *Baccharis linearis* and *Muehlenbeckia hastulata* (cover 53%) and (ii) "closed" sites, located under the canopy of patches of vegetation dominated by *C. alba* (cover 95%). The period of seed dispersal in *C. alba* ranges from March to July (Autumn-Winter) and seedling establishment ranges from September to October (Spring). Preliminary evidence suggests that this species has no seed bank, e.g., seeds remain viable only for 4 months. Therefore, if there is no germination during this time, seeds suffer desiccation and die.

### Seed and seedling abundance

We determined the seed and seedling abundances of *C. alba* in both open and closed habitats. The number of seeds was counted by removing and sieving 100 cm<sup>3</sup> of soil from 200 randomly located plots. 100 samples were obtained from each habitat type. The number of seedlings was estimated by placing 360 quadrants of 0.25 m<sup>2</sup>, 180 per habitat type.

### Foxes legitimacy

We evaluated the germination in fox-defecated seeds versus control seeds, under laboratory conditions. During May 1988 we collected 150 seeds from 20 fresh scats over different habitats and 150 seeds from intact fallen fruits under 10 parental trees (DBH > 10 cm). Seeds from each source were pooled before the experiments in order to homogenize the sample. We also included a sample of 50 fox-defecated and 50 control seeds from a different area, Río Clarillo (Andean Range, 33°44'S, 70°28'W) collected using the same procedure. Seeds were placed in Petri dishes (10 per dish) containing sterile sand, and were watered as needed. Experiments were performed in darkness at  $25 \pm 1^\circ\text{C}$ . Germination was checked periodically, until no further germination was detectable. Duration of each experiment was 83 days for the sample from El Pangue, and 61 days for the sample from Río Clarillo. We considered a seed "germinated" if it had a radicle at least 5 mm of length.

### Foxes efficiency

This evaluation was carried out only at El Pangue during July and September 1989. We determined seed defecation by foxes, seed germination and seed predation in both open and closed habitats. We collected 40 whole feces, noting whether they contained *C. alba* seeds and the habitat in which each scat has been deposited. Feces were collected while walking by randomly selected routes which crossed the two habitat types. We observed *C. alba* germination regarding to both habitat and dispersal agent: gravity and fox. Gravity is considered a legitimate dispersal agent for most plant species (barochory *sensu* VAN DER PIJL, 1982). We considered a seed fox-defecated if it was immersed in a scat; seeds of intact fruit fallen by gravity were checked under parent trees. We considered a fallen fruit intact if it had no sign of damage or rot on its cover. A test for independence between germination, dispersal agent and habitat was performed through a multi-way contingency table (SOKAL & ROHLF, 1981). This method requires that observations are independent of each other. For clumped seeds in scats, we assumed that the germination of a particular seed is not affected by the vicinity of the other seeds. We also checked seed predation in *C. alba*. In July 1989, we compared the proportion of seeds removed in open and closed habitats. We placed 15 plastic Petri dishes, 10 seeds per dish, in both habitat types, during 4 days. At the end of the experiment, we counted the number of seeds remaining per dish. In these experiments, seed removal was assumed equivalent to seed consumption (WEBB & WILLSON, 1985).

## RESULTS

### Seed and seedling abundance

Seeds of *C. alba* in the soil were found only in closed habitat. On average,  $0.7 \pm 0.1$  seed/100 cm<sup>3</sup> of soil were found under the canopy of trees and shrubs. Seedlings of *C. alba* were also largely restricted to closed habitats: 49 (96.1%) were growing under the canopy while only 2 (3.9%) were found in the openings.

### Foxes legitimacy

Germination was significantly higher among fox-defecated seeds than gravity fallen seeds at El Pangue (proportion test,  $P < 0.001$ ) and at Río Clarillo (proportion test,  $P < 0.001$ ) (see table I). Additionally, fox-defecated seeds begun germination by the 4 th day of experiment while control seeds begun germination after a fortnight.

### Foxes efficiency

At El Pangue, we collected 40 whole *D. culpaeus* scats, 32.5% of which contained a total of 212 *C. alba* seeds. Scats of *D. culpaeus* were more common in open than in closed habitat, despite a similar sampling effort on both habitats. Thirty scats (75%) and 150 seeds from scats (71%), were found in

TABLE I. — *Percentage of germination in seeds collected from feces of Dusicyon culpaeus and under parental trees (control) of Cryptocarya alba, El Pangué and Río Clarillo. N=sample size.*

	Control		Fox-defecated		Z	P (*)
	%	N	%	N		
El Pangué	10.6	150	40.7	150	9.28	<0.001
Río Clarillo	2.0	50	82.0	50	7.42	<0.001

(\*) Proportion test.

open habitat. Germinated seeds were more frequently found in closed than in open habitats (31.6 vs 3.2%). Additionally, germination was more frequent in gravity-fallen seeds than fox-dispersed seeds (77.3 vs 22.7%). However, in closed habitats, the frequency of germinated seeds was not different between the two dispersal agents. However, in open habitat fox-dispersed seeds germinated in higher

TABLE II. — *Percentage of germinated seeds of C. alba regarding habitat: open versus closed, and dispersal agent: fox or gravity. n = total number of seeds (germinated or not).*

Habitat	Dispersal agent				Total	n
	Fox	n	Gravity	n		
Open	7.6	105	1.9	364	3.2	469
Closed	36.5	104	30.2	354	31.6	458
TOTAL	22.7	209	77.3	718	100.0	917

proportion than gravity-dispersed seeds (table II). Overall, the multi-way contingency analysis showed that germination was strongly dependent on habitat ( $P \ll 0.001$ ) but independent of the dispersal agent

TABLE III. — *Three-way test of independence (SOKAL & ROHLF, 1981) for germination of Cryptocarya alba seeds collected from feces of foxes and under parental trees in open and closed habitats.*

Hypothesis (Ho)	df	G	P
(a) Independence germination × disperser	1	2.6	>0.100
(b) Independence germination × habitat	1	160.3	$\ll 0.001$
(c) Independence disperser × habitat	1	>0.1	>0.500
(d) Interaction between germination × disperser × habitat	1	5.1	<0.030
(e) Independence of germination × disperser × habitat	4	168.0	$\ll 0.001$

( $P > 0.1$ ) (see table III). Finally, seed removal of *C. alba* was significantly higher in open habitats (mean proportion of removed seed  $\pm$  1 s.e.;  $0.51 \pm 0.03$ ) than in closed habitats ( $0.23 \pm 0.03$ ; Wilcoxon,  $P \ll 0.001$ ).

## DISCUSSION

Laboratory evidence show that *D. culpaeus* defecates viable seeds of *C. alba* which germinate earlier and in a higher proportion than control seeds. These results suggest that (i) foxes are legitimate dispersers (seeds are not damaged) and (ii) it

is beneficial for seed germination to be ingested by foxes. In fact, it has been suggested that factors which enhance and improve germination, subsequently increase survival and recruitment (HARPER, 1977; JONES & SHARITZ, 1989). This fact ought to be relevant for species with short-lived seeds as the case of *C. alba*. However, field evidence, that is, the higher frequency of dispersed seeds into open habitats and the prevalence of habitat over disperser for germination, reveal that foxes are "inefficient" dispersers of *C. alba*, as they often disperse seeds in "unsafe sites". In fact, *D. culpaeus* transport seeds away from parental plants and thus modify the seed shadow of *C. alba*, enlarging the distribution tails. Seeds are deposited in open habitats, where they would not normally occur if dispersed by gravity alone. In these habitats, germination and survival is restricted by desiccation and seed predators.

In this study, we did not measure foxes effectiveness, that is, what proportion of seedlings come from fox-defecated seeds (REID, 1989). The higher proportion of germinated seeds from fox-defecated seeds in openings (see table II) suggests that at least during rainy years, some seedlings could sprout from seeds dispersed by foxes. However, evidence suggests that open habitats are also "unsafe sites" for seedlings. In fact, desiccation and herbivory are limiting factors for seedling establishment in many species of the matorral (*C. alba* included, FUENTES *et al.*, 1984).

Therefore, foxes are legitimate dispersers because they do disperse viable seeds. Nevertheless, they are inefficient and possibly ineffective dispersers because they deposit viable seeds where germination, seed- and seedling survival is unlikely.

In short, the general assumption of the beneficial effects of seed dispersers on plant fitness is rejected by our data. Clearly, the criteria of association seed-scat is insufficient to determine the nature of the animal-plant interaction, and both lab and field evidence should be simultaneously considered while assessing the legitimacy and efficiency of foxes or other vertebrates as seed dispersers.

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