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## Rabbits (*Oryctolagus cuniculus*) select small seeds when feeding on the fruits of *Corema album*

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**Abstract** Herbivores are hypothesized to consume fruits and seeds while foraging on the vegetative parts of plants. A small seed size is an important condition for this foliage-as-fruit hypothesis to be proved, but has received little attention at the intra-specific level. We measured *Corema album* seeds ingested by rabbits and those collected from plants and found that rabbits are actively selecting for small seeds. The mechanisms of this selection remain unclear, although my results discard (1) the phenology of consumption, (2) effects of gut passage, and (3) intra-plant heterogeneity of seed sizes as possible mechanisms.

**Keywords** Seed dispersal · Seed-size selection · Rabbit · Fleshy fruits · Endozoochory

### Introduction

Janzen hypothesized that some plant species with small seeds may resort to foliage in order to attract large herbivores that will eat their fruits and hence disperse their seeds (Janzen 1984). From then on, seed dispersal by herbivores has been usually analyzed in the context of the ‘foliage-as-fruit’ hypothesis. Certainly, herbivores seem to disperse mostly small-seeded species with no apparent dispersal structures, which are presumably eaten while grazing or browsing (Malo and Suárez 1995; Pakeman et al. 2002; Eycott et al. 2007).

Central to this hypothesis is the importance of seed size for dispersal, which has attracted the attention of researchers, with conflicting results up to now. While in general herbivores seem to disperse mostly small-seeded species, at a more detailed local scale the relationship between a small seed size and the probability of dispersal

for a given plant species is far from clear (Pakeman et al. 2002).

Despite this interest in analyzing seed-size effects at the inter-specific level, its role within a single plant species (at the intra-specific level) has seldom been addressed. However, seed size has been proven to play an important role in shaping plant–disperser interactions for other groups of dispersers, either affecting fruit selection by dispersers (Wheelwright 1993; Stanley and Lill 2002; Alcántara and Rey 2003), or limiting maximum dispersal distance, both directly (Muñoz and Bonal 2008) and through effects over gut treatment (Traveset et al. 2008). On the other hand, disperser selection of seed size will condition germination, growth, and survival of seeds (Gómez 2004).

Lagomorphs have often been disregarded when studying endozoochory, even when considering dispersal by herbivores, despite the fact that several authors have reported them as effective seed dispersers (Zedler and Black 1992; Malo and Suárez 1995). Recent studies, however, have remarked the role of lagomorphs and especially rabbits (*Oryctolagus cuniculus*) as important seed-dispersal agents (Pakeman et al. 2002), playing a more prominent role at a local scale than large herbivores (Eycott et al. 2007).

As part of a wider study on fruit and seed-size variation on *Corema album*, I analyzed fruit consumption by rabbits in the north-western Iberian Peninsula, with the aim of knowing whether rabbits select for seed size when feeding on *Corema* fruits. Rabbits are known to eat fruits of *C. album* and disperse their seeds (Calviño-Cancela 2002). As apparent seed-size selection could be derived from an effect of gut passage on ingested seeds, I addressed seed-size selection by firstly testing if the seeds defecated by rabbits in the field were of a different size than those collected from the plants and, secondly, if seed size changed as a consequence of ingestion and gut treatment. *Corema album* fruits are much smaller than the gape width of rabbits, and hence I did not expect there to be a seed-size selection due to this reason. However, seed-size selection could be unintentional, and

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result as a consequence of the interaction between foraging behavior and spatio-temporal seed-size heterogeneity. Hence, I explored two potential mechanisms for apparent seed selection: (1) phenology of consumption (eating fruits when seeds are still unripe) and (2) within-plant spatial heterogeneity on fruit size.

## Methods

### Study site and species

*Corema album* (D.) Don in Sweet, 1830 (Empetraceae) is a small long-lived shrub of up to 1 m height that grows in coastal dune habitats of the Iberian Peninsula (ssp. *album*) and Azores Islands (ssp. *azoricum* Pinto da Silva). The continental subspecies spreads all along the Iberian Peninsula Atlantic coast, from Ferrol (A Coruña, northwestern Spain) to Cadiz (southern Spain). *Corema album* is a wind-pollinated, dioecious species that flowers from March to April (Guitián et al. 1997). Females set hundreds to thousands of white, almost spherical drupes that take months to ripen (Guitián et al. 1997). The first ripe fruits appear during the first week of August, but fruit availability peaks in mid-September (Larrinaga, unpublished data). Each fruit measures up to 1 cm in width (mean length 8.16 mm, mean width 9.54;  $n = 199$ ) and contains usually three small seeds (mean length 3.75 mm, mean width 2.81 mm;  $n = 295$ ), protected by a hard woody endocarp. Seed size is positively correlated to fruit size (seed-to-fruit weight  $r = 0.5757$ ,  $P < 0.001$ ,  $n = 99$ ). Gulls, blackbirds, and rabbits have been cited as its main dispersers in an Atlantic island (Calviño-Cancela 2002), but carnivores are also known to feed on these fruits (Larrinaga, unpublished data).

The study area is located at Praia Trece, northwestern Spain (A Coruña; 9.1484°W, 43.1865°N; WGS84), showing an Atlantic climate, with a mean temperature of 13°C and annual precipitation of around 1,500 mm. The *C. album* population spreads along the dunes of a beach-dune-lagoon system and up the slope of an adjacent climbing dune.

### Phenology of seed consumption

To assess if rabbits were eating *Corema* fruits when still unripe, rabbit fecal pellets were collected in Trece Beach, both 1 month before fruit ripening and during the period of maximum fruit availability in 1994. One month before fruit ripening (July 5) 165 fecal pellets were collected from a total of seven different latrines, all of them within an area where *C. album* is the dominant plant species. A few weeks later (August 27), once *Corema* fruits were ripe, 484 additional fecal pellets were gathered from seven latrines in the same area. All pellets were disintegrated by hand and the number of *Corema*

seeds per pellet recorded. No broken seeds were ever found in rabbit pellets.

### Seed-size selection

I selected ten plants at regular intervals along a randomly drawn transect across the *C. album* population. One hundred fruits from each selected plant were collected and hand-squeezed to extract the seeds. Seeds from rabbit pellets and those from fruits were measured with a digital calliper (length and width) to the nearest 0.01 mm and weighed to the nearest milligram.

In order to rule out a possible change in seed size due to the passage through the rabbit's gut, a seed-ingestion experiment was carried out in 2000 with four captive rabbits. Rabbits were hybrid individuals coming from domestic and wild parents and were kept in standard breeding cages by the Game Department of the Regional Government. I collected a variable number of fruits from eight plants at Trece Beach. Fruits were mixed and I randomly selected 200 of them. I fed each rabbit 40 of these fruits, keeping the remaining 40 as controls. Animals were not deprived of their food and they were allowed to feed freely on the provided fruits. Control fruits were hand-squeezed and their seeds measured and weighed, following the same methodology used in 1994. Rabbit pellets from the four cages were collected during 1 week. Due to the design of the cages we had no way to monitor the number of eaten fruits per individual nor to assure that all defecated seeds were collected. Mean number of seeds retrieved per rabbit was 28.3, and actually only data from three rabbits were analyzed, due to small sample size for the fourth individual. Seeds were retrieved by hand and later measured to the nearest 0.01 mm and weighed to the nearest 0.1 mg.

### Intra-plant variation on seed size

Due to rabbits feeding only upon the lower part of *Corema* plants, which can reach up to 1 m in height, we sampled fruits from both the lower and upper parts of several plants in 2000. We selected the same plants previously used in 1994, except for two that were not relocated. In each of these plants we collected a sample of ten fruits from the lower part of the plant (one-third of its height) and another ten fruits from the upper part (the highest third of its height). Fruits were hand-squeezed and their seeds extracted and later measured with a digital calliper to the nearest 0.01 mm and weighed to the nearest 0.1 mg.

### Statistical analysis

All analyses were carried out using multivariate ANOVAs, with treatment (either ingested vs. non-ingested or upper vs. lower part or plant) as fixed factor. When

comparing seeds from the lower versus the upper part of plants, plant was introduced as a random factor, and its interaction with the type of treatment was also considered. Post-hoc analysis was carried out variable by variable, in a univariate approach. SPSS 16.0 and SAS 9.1 were used for statistical analyses.

## Results

### Seed-size selection

Seeds from rabbit pellets were significantly smaller than those collected from the plants (Wilk's  $\lambda = 0.853$ ,  $F_{3,390} = 22.333$ ,  $P < 0.001$ ). This difference holds for the three measured variables, length, width, and weight of seeds ( $F_{1,392} = 16.481$  and  $P < 0.001$  for all three variables; Fig. 1).

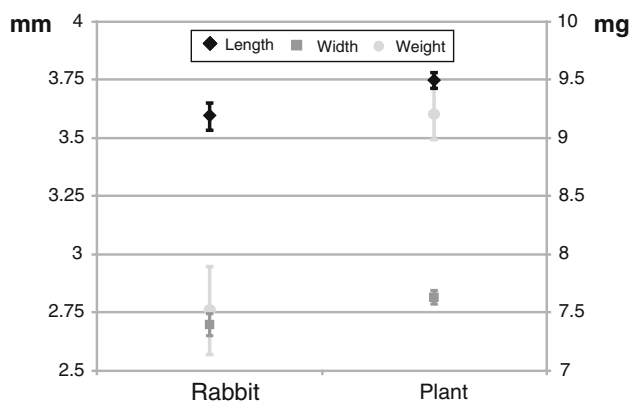
Differences in size between seeds from rabbit pellets and seeds from plants were not due to an effect of gut passage, since no change of seed size was found for defecated seeds in the feeding experiment with captive rabbits (Wilk's  $\lambda = 0.992$ ,  $F_{3,198} = 0.565$ ,  $P = 0.639$ ).

### Phenology of seed consumption

No seeds or other *Corema* remains were found in the fecal pellets collected 1 month before fruit ripening, while in August, month of maximum fruit availability, 28.71% of the collected pellets contained at least one *Corema* seed. Pellets contained an overall mean of  $0.94 \pm 2.07$  (mean  $\pm$  SD) seeds. The maximum number of *Corema* seeds per pellet was 14.

### Intra-plant variation on seed size

Seeds coming from the upper part of plants were not significantly different from seeds found in the lower part



**Fig. 1** Estimated measures for *Corema album* seeds, coming from rabbit pellets and collected from the plants. Error bars indicate 95% confidence intervals

(Table 1), although the significance of the interactions suggests that this is so for some of the individuals. In fact, some of the plants seem to bear smaller fruits in the lower part, while others bear bigger or similar fruits.

## Discussion

Rabbits seem not to fit to the 'foliage-as-fruit' hypothesis, but rather to be actively searching for *Corema* fruits, as they do not feed on them until they are ripe. This is supported by the fact that leaf remains were found only in one of a total of 649 pellets analyzed and by the high amount of fruits eaten per rabbit and day (36–109 g, as estimated from the frequency of seeds per pellet; see below). Probably this is also the case for other fleshy fruits reported to be consumed by this species (Muñoz-Reinoso 1993; Nogales et al. 1995) and perhaps for some non-fleshy fruits (D'Antonio 1990; Pakeman et al. 1999; Eycott et al. 2007).

Rabbits defecate between 204 and 917 pellets per day (Simonetti 1989), which according to my data could result in between 192 and 862 *Corema* seeds dispersed per day and rabbit. These figures are much higher than the number dispersed by rabbits in acidic grasslands (Pakeman et al. 1999: 30–150 seeds per day), although similar figures have been reported for other European habitats (Malo and Suárez 1995: 500 seeds per day, Eycott et al. 2007: 333–820 seeds per day). Seed abundance per pellet was also similar to that reported by Calviño-Cancela (2002: 0.97 seeds per pellet) for the same species at a nearby site, although much higher than that reported by Zedler and Black (1992: 0.087 seeds per pellet).

Rabbits selected small seeds when feeding on *Corema* fruits. Seed passage could selectively affect survival of different sized seeds (Pollux et al. 2007) or could change seed traits by hydrating, drying, or eroding the seeds (Traveset et al. 2008). However, in this case, the size of *Corema* seeds defecated by rabbits was similar to that of non-ingested ones, suggesting there is no cryptic selection of seed size or a change of seed traits in the rabbit gut. On the other hand, if seeds were smaller in the lower part of the plant, the one accessible to rabbits, they would be actually dispersing seeds smaller than average. However, in Praia Trece, this does not seem to be the case.

Results suggest that rabbits are actively selecting fruits with smaller seeds than the average, either by selecting the plant with the smallest fruits or by selecting small fruits within plants. Fruit-size selection is common among disperser animals, resulting in seed-size selection due to the positive correlation between fruit and seed size commonly found. Selection for bigger fruits is probably the commonest case (Wheelwright 1993; Gómez 2004). However, negative seed-size selection has also been reported, although usually it has been mostly related to gape width constraints or other physical limitations arising from seed/body size (Alcántara and Rey 2003; Muñoz and Bonal 2008). Rabbits do not show this type of constraint when feeding on *C. album* fruits,

**Table 1** Results of the multivariate ANOVA relating seed size with position in the plant (upper or lower)

	Wilk's $\lambda$	<i>df</i>	<i>df</i> <sub>err</sub>	<i>F</i>	<i>P</i>
Multivariate					
Position	0.9561	3	142	2.17	0.0937
Plants	0.1231	21	408.3	20.88	< 0.0001
Position $\times$ plant	0.7612	21	408.3	1.94	0.0081
	MS	<i>df</i>	<i>df</i> <sub>err</sub>	<i>F</i>	<i>P</i>
Seed length					
Position	0.0233	1	7	0.09	0.7774
Plants	1.0539	7	144	14.02	< 0.0001
Position $\times$ plant	0.2697	7	144	3.59	0.0014
Seed width					
Position	0.0664	1	7	0.76	0.4122
Plants	0.7321	7	144	23.60	< 0.0001
Position $\times$ plant	0.0874	7	144	2.82	0.0088
Seed weight					
Position	0.0000	1	7	0.00	0.9975
Plants	45.0024	7	144	16.93	< 0.0001
Position $\times$ plant	5.8948	7	144	2.22	0.0360

Results from post-hoc univariate ANOVAs are also shown

which are always smaller than 11 mm. Selection for small seed size in animals that do not face physical constraints for the ingestion or digestion of seeds is much rarer (Pollux et al. 2007). Fruit size being equal, selection against seed load of fruit (Stanley and Lill 2002), which imposes important costs to fruit digestion, would lead to selection for small seeds. Alternatively, rabbits could be selecting for some other quality trait of fruits that, being correlated to seed size, would provoke the selection of small-seeded fruits (Avery et al. 1993).

Further research with wild captive rabbits, aiming at describing fruit preference in rabbits and the criteria underlying fruit choice, would help us understand the ultimate causes for the observed seed size selection. Anyway, whatever the underlying cause, the net effect of rabbits feeding on *C. album* fruit is to favor the dispersal of small seeds. If rabbit dispersal alters the pattern of seed survival, germination and emergence, this could result in selective pressures exerted by this disperser on seed size of *C. album*.

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## References

- Alcántara JM, Rey P (2003) Conflicting selection pressures on seed size: evolutionary ecology of fruit size in a bird-dispersed tree, *Olea europaea*. *J Evol Biol* 16:1168–1176
- Avery ML, Goocher KJ, Cone MA (1993) Handling efficiency and berry size preferences of cedar waxwings. *Wilson Bull* 105(4):604–611
- Calviño-Cancela M (2002) Spatial patterns of seed dispersal and seedling recruitment in *Corema album* (Empetraceae): the importance of unspecialized dispersers for regeneration. *J Ecol* 90:775–784
- D'Antonio CM (1990) Seed production and dispersal in the non-native, invasive succulent *Carpobrotus edulis* (Aizoaceae) in coastal strand communities of central California. *J Appl Ecol* 27:693–702
- Eycott AE, Watkinson AR, Hemami MR, Dolman PM (2007) The dispersal of vascular plants in a forest mosaic by a guild of mammalian herbivores. *Oecologia* 154:107–118
- Gómez JM (2004) Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. *Evolution* 58(1):71–80
- Guitián P, Medrano M, Rodríguez M (1997) Reproductive biology of *Corema album* (L.) D. Don (Empetraceae) in the northwest Iberian Peninsula. *Acta Bot Gallica* 144(1):119–128
- Janzen DH (1984) Dispersal of small seeds by big herbivores: foliage is the fruit. *Am Nat* 123:338–353
- Malo JE, Suárez F (1995) Herbivorous mammals as seed dispersers in a Mediterranean dehesa. *Oecologia* 104:246–255
- Muñoz A, Bonal R (2008) Are you strong enough to carry that seed? Seed size/body size ratios influence seed choices by rodents. *Anim Behav* 76:709–715
- Muñoz-Reinoso JC (1993) Consumo de gálbulos de sabina (*Juniperus phoenicea* ssp. *turbinata* Guss, 1891) y dispersión de semillas por el conejo (*Oryctolagus cuniculus* L.) en el Parque Nacional de Doñana. Doñana. *Acta Vert* 20(1):49–58
- Nogales M, Valido A, Medina FM (1995) Frugivory of *Ploclama pendula* (Rubiaceae) by the rabbit (*Oryctolagus cuniculus*) in xerophytic zones of Tenerife (Canary Islands). *Acta Oecol* 16(5):585–591
- Pakeman RJ, Engelen J, Attwood JP (1999) Rabbit endozoochory and seed bank build-up in an acidic grassland. *Plant Ecol* 145:83–90
- Pakeman RJ, Digneffe G, Small JL (2002) Ecological correlates of endozoochory by herbivores. *Funct Ecol* 16:296–304
- Pollux BJA, Ouborg NJ, Van Groenendael JM, Klaasen M (2007) Consequences of intraspecific seed-size variation in *Sparganium emersum* for dispersal by fish. *Funct Ecol* 21:1084–1091
- Simonetti JA (1989) Tasas de defecación y descomposición de fecas de *Oryctolagus cuniculus* en Chile central. *Medio Amb* 10(1):92–95

- Stanley MC, Lill A (2002) Importance of seed ingestion to an avian frugivore: an experimental approach to fruit choice based on seed load. *Auk* 119(1):175–184
- Traveset A, Rodríguez-Pérez J, Pías B (2008) Seed trait changes in dispersers' guts and consequences for germination and seedling growth. *Ecology* 89(1):95–106
- Wheelwright NT (1993) Fruit size in a tropical tree species: variation, preference by birds, and heritability. *Vegetatio* 107/108:163–174
- Zedler PH, Black C (1992) Seed dispersal by a generalized herbivore: rabbits as dispersal vectors in a semiarid California vernal pool landscape. *Am Midl Nat* 128:1–10