Ann. Zool. Fennici 47: 195–205 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 30 June 2010

The role of carnivores as Mediterranean seed dispersers

Luís M. Rosalino*, Sílvia Rosa & Margarida Santos-Reis

*Universidade de Lisboa, Centro de Biologia Ambiental, Faculdade de Ciências de Lisboa, Departamento de Biologia Animal, Ed. C2, 1749-016 Lisboa, Portugal (*e-mail: lmrosalino@fc.ul.pt)*

Received 20 July 2009, revised version received 24 Nov. 2009, accepted 24 Nov. 2009

Rosalino, L. M., Rosa, S. & Santos-Reis, M. 2010: The role of carnivores as Mediterranean seed dispersers. — *Ann. Zool. Fennici* 47: 195–205.

Seed dispersal by vertebrates is one of the main plant–animal interactions, especially in the Mediterranean region where fleshy fruits are, at least seasonally, one of the main food resources for birds and carnivores. To effectively assess the role of these predators as seed dispersers, we need to demonstrate the viability of ingested seeds. We therefore compared germination rates of seeds from freshly collected fruits with those of seeds collected from carnivore scats. We detected that several species (e.g. badgers, foxes, genets) had a significant positive effect on germination rates of seed of at least one fruit pland and one species (stone marten) had deleterious effects on most seeds. Seed size (e.g. weight, width, etc.) was correlated with seed survival, germination time and germination rate.

Introduction

Animal–plant interactions and their co-evolution, especially with regard to seed dispersion, give rise to some of the most interesting ecological research questions in understanding ecosystem regeneration and evolution (Corlett 1995). These dispersal events can play an important role in population expansion, the exchange of individuals between populations and the colonization of vacant habitats (Nathan *et al*. 2008). Moreover, long-distance dispersal has a particular marked influence on ecosystems, and carnivorous mammals are one of the most important vertebrate groups involved in longer dispersal distances (Jordano *et al*. 2007). Dispersal affects large-scale phenomena of great conservation concern, such as the spread of invasive plants, range shifts following climate change and persistence of species in fragmented landscapes (Nathan *et al*. 2008). An important number of plants, usually fleshy-fruited, have developed a mutualist relationship with animals (vertebrates and invertebrates, *see* e.g. Shanahan *et al*. 2001) to assure seed dispersion (e.g. Corlett 1998). Vertebrates represent the main group of fruit eaters, digesting the pulp but passing the seeds almost unchanged and ready to germinate (Herrera 1995). To be an effective seed disperser, seed's passage through a vertebrate gut should enhance germination, i.e., increase the rate of germination and/or the proportion of seeds that germinate, or at least have a neutral effect on the seed's viability (Traveset 1998). Traveset's (1998) review on the effect of seed passage through vertebrate frugivores' guts reports that in 39% of the studies with non-flying mammals, there was evidence that fruit consumption enhanced germination, while only 19% described inhibition of germination (42% showed no effect). Several explanations are given to explain how the fruit passage through the vertebrate digestive system favours seed germination: (1) separation of seeds from the pulp in fleshy fruits, (2) moistening and fertilization conferred by faecal material present in the dung, and (3) softening and scarification of the seed coat through mastication or action of acids and enzymes in saliva and stomach secretions (Razanamandranto *et al*. 2004).

In the Mediterranean region, most plants producing fleshy-fruits are dispersed by birds or by an association of carnivores and birds (Herrera 1995). Birds are usually considered the main plant dispersers in southern Europe, although evidence for a common history of interaction is lacking (Herrera 1995) and, excluding migratory movements, they are mainly short-distance dispersers (Schaumann & Heinken 2002). Several carnivores are also considered seasonal dispersers, because fruits are an important part of their diet (e.g. Rosalino & Santos-Reis 2002, Rosalino *et al*. 2005, Santos *et al*. 2007). For example in Spain, three species of carnivores (red fox, Eurasian badger and stone marten) are responsible for dispersing 40% of the fleshy-fruit seeds (Herrera 1995). Due to their importance, in extreme situations involving local extinction of carnivores, the dispersal of seeds between plant populations may decrease, potentially leading to the isolation of the seed producing populations (Jordano *et al*. 2007).

To confirm the role of carnivores as fruit dispersers it is necessary to validate the consumption of fruit by these species, and also to test if seeds that have been subjected to the digestive process are still viable and capable of successful germination. Many studies have focused on the first approach (e.g. Pigozzi 1992, Rosalino & Santos-Reis 2009), but few have examined the success of germination following consumption by Mediterranean carnivores (e.g. Traveset *et al*. 2001, Schaumann & Heinken 2002, Verdú & Traveset 2004).

Our study goals were to: (1) compare the effect of several species of carnivore dispersers on germination success of typical Mediterranean fleshy-fruits, and (2) evaluate the factor(s) enhancing/constraining fruit germination rates.

Material and methods

Study area

The field study was conducted in Serra de Grândola, a coastal mountain area of southwestern Portugal (38°6´N, 8°34´W), characterized by a semi-arid climate (Mediterranean type), with mild winters and hot, dry summers (Correia & Santos-Reis 1999). The landscape is dominated by 'montado' matrix (cork oak woodland), interspersed with a mosaic of small habitat patches including orchards, olive groves and riparian vegetation. The area sustains a high diversity of wild, semi-wild and cultivated fruit species: blackberries (*Rubus ulmifolius*), Mediterranean smilax (*Smilax aspera*), strawberry tree (*Arbutus unedo*), pears (*Pyrus bourgaeana*), plums (*Prunus* sp.), apples (*Malus* sp.), figs (*Ficus carica*), garden tomato (*Solanum lycopersicum*), loquats (*Eriobotrya japonica*), olives (*Olea europaea*) and vine grapes (*Vitis vinifera*). These fruits are used by most vertebrates inhabiting the mountain, including carnivores (Rosalino *et al*. 2005, Santos *et al*. 2007). More than 64% of all Portuguese carnivore species occur in Serra de Grândola (Santos-Reis *et al*. 1999), including foxes (*Vulpes vulpes*), weasels (*Mustela nivalis*), polecats (*Mustela putorius*), stone martens (*Martes foina*), Eurasian badgers (*Meles meles*), Eurasian otters (*Lutra lutra*), common genets (*Genetta genetta*) and Egyptian mongooses (*Herpestes ichneumon*).

Field methods

Carnivore scat samples from red foxes, weasels, stone martens, Eurasian badgers, common genets and Egyptian mongooses were collected from linear transects between February 2006 and January 2007. Samples were collected on a monthly basis after an initial clearance (January 2006) to allow a more precise estimate of scat's time of deposition. Three transects, with a total length of 7.5 km, were set to proportionally include all landscape types of the study area. Collected scats were identified to species (using scats' morphological and scent characteristics, based on researchers experience and described features, *see* Macdonald & Barrett 1993), tagged, and later analysed in the laboratory. Although the use of field-collected scats has been the subject of some criticism (e.g. Reynolds & Aebischer 1991), this approach is still frequently used (e.g., Virgós *et al*. 2002, Moreno *et al*. 2006, Santos *et al*. 2008, Matos *et al*. 2009); the assemblage of species inhabiting southern Mediterranean areas produce distinguishable scats (on the basis of size, shape, odour and location) and miss-identification errors are minimized by the rareness of closely related species (e.g. weasels *Mustela nivalis* and polecats *Mustela putorius*, whose scats could be potentially confounded with those of stone martens *Martes foina*).

Six species of fruit-bearing plants were selected according to seeds visually identified in scats: blackberries, figs, olives, pears, strawberry tree, and vine grapes. For each species, five fruits from 20 randomly chosen individual plants were collected.

Laboratory experiment

After collection, scat samples were immediately processed following standard analytical procedures (e.g. Rosalino & Santos-Reis 2002). Date of collection was recorded (to be used as a surrogate for consumption date), and all seeds found in the samples were separated from the remaining non-digested material, species identified, weighed and measured (length and width). Other consumed prey (mammals, birds, reptiles, amphibians, eggs, arthropods, gastropods and other plant material) were also identified on the basis of the visible remains, to roughly assess meal composition (trophic diversity). Subsequently, following Baskin and Baskin (1998), each seed was cultivated in a 4 × 4 × 5 mm pit-cell, filled with a mixture of peat and river sand, and kept in a germination tray with controlled conditions of sunlight and water. Each pit-cell was monitored and irrigated twice a week and emergence date was recorded (defined as the date when the seedling emerged above the cell surface).

Fresh fruits collected in the field, under tree canopy and still intact (< 15–20 days after ripening) were also weighed and measured (length and width) prior to seed extraction. Each of these seeds was subjected to the same procedure as those collected in scats.

The number of days to emergence for both seed types (from scats or fruit plants) was the number of days from planting to germination.

Data analysis

We used three different analytical approaches to ascertain the role of carnivores as Mediterranean fruit dispersers. First, for each carnivore species we compared the percentage of germinated seeds for each fruit per carnivore, using Yates' correction for continuity applied to a modified chi-square test (Simpson *et al*. 1960).

Then, we assessed potential factors influencing seed germination (the response variable), including those related to the consumer (carnivore species and its dietary diversity, estimated as the number of food types in the scat where the seed was collected), and those associated with the fruit and its seeds, specifically fruit type, field collection date, seed size (weight, length and width) and seed shape (ratio width/length). We tested three hypotheses: germination was determined by (1) carnivore-related factors, (2) seed characteristics, and (3) combination of both. For this purpose, following Hosmer and Lemeshow (1989) we used Logistic Regression models (binomial distribution and logit link function). This statistical procedure allows the analysis of binary response variables [germination(1)/no germination(0)] (Zuur *et al*. 2007). Models were developed for each fruit species and for all fruit types pooled together. Model selection was based on Akaike information criterion (AIC, ΔAIC and WI)

Since this technique is very sensitive to multicollinearity of independent variables (Tabachnick & Fidell 1996), we tested correlations between them using Spearman's rank correlation (r_s) (Zar 1999). Cook's distance was used to investigate outliers (Maroco 2007). When correlations between pairs of variables were detected, the one that showed a higher association with the response variable (on the basis of the significance value of the Wald statistics) was retained for further analysis.

Significance of regression parameters was tested using the Wald statistic and the likelihood ratio test. Models' goodness-of-fit was assessed using: (i) percentage of correct classifications, and (ii) Pearson residuals chi-square test. Lastly, the effect of seed size (weight, length and width) and origin (scat or fruit samples) on germination rate (i.e. difference, in days, between the planting and emerging at the cell surface dates) and their interactions per species, was evaluated using a general linear model (GLM) (Tabachnick & Fidell 1996). For each GLM, the equality of error variances was tested using Levene's test and the normality of residuals was tested using a Kolmogorov-Smirnov (K-S) test (Zar 1999). Since the model for strawberry tree fruits did not produce normally distributed residuals, even after data transformation, a Generalized Linear Model was used (Zuur *et al*. 2007). All analyses were carried out using SPSS for Windows, ver. 16.0.1.

Results

During the 12 months of field work, 326 scats were collected: 7 of weasels, 47 of stone martens, 107 of Eurasian badgers, 35 of Egyptian mongooses, 97 of common genets and 33 of red-foxes. From those, only 171 contained seeds (weasel: 1; stone marten: 24; badger: 60; Egyptian mongoose: 18; genet: 46; fox: 22). Due to small sample size, weasel data were excluded from further analyses. Data regarding fruits, seeds and carnivores are summarised in Table 1.

The comparison between the proportion of germinated seeds collected from the field and those that have passed through the carnivores' digestive tracks showed that some mammalian species have a positive effect on germination, while others negatively influence germination (Table 2). Thus, while consumption of pears by badgers, genets and foxes; olives by badgers and genets; and grapes by genets seemed to promote their seed germination, the remaining combinations of seeds and carnivores had deleterious effects on germination (Table 2). With regard to figs, although several statistical differences were detected, (e.g., higher germination rate if figs are consumed by genets), due to very low percentage recorded (< 0.001, Table 2) we ignored this result.

When all seeds were pooled together, it was clear that the probability of germination was influenced by the seed weight, consumption date and fruit species considered (Table 3). The detection of multicollinearity prevented the use of seed length, width and shape in logistic regression models. Due to small sample sizes some of the fruits were not included in the models; analysis was only possible for pears, figs and olives. For figs, the number of prey types in the meal seemed to positively influence germination (Table 4). Pear germination appears to be constrained by carnivore species (especially stone martens), and heavier seeds are more likely to germinate (Table 5). Finally, olive germination is more likely from heavier seeds consumed later in the year (Table 6). Models showed that at least one independent variable had predictive power for each fruit species, and demonstrated a fair to good goodness-of-fit whatever the method used (Tables 3–7).

Due to small sample sizes, GLMs were only produced for pears, figs and olives. None of the considered variables seemed to influence olive's germination rate. For pears, the germination rate was dependent on the interaction carnivore species × origin × seeds width ($F_5 = 18.629$, $p < 0.001$; Levene's test: $F_{4,5} = 1.027$, $p = 0.402$; K-S test: $Z_{59} = 1.328$, $p = 0.059$). Figs were highly affected by seeds' width ($F_1 = 5.887$, $p = 0.027$; Levene's test: $F_{1,2} = 0.023$, $p = 0.881$; K-S test: $Z_{19} = 0.858$, $p = 0.453$). However, models did not account for much of the variability present in the data. For example for figs, GLM explained only 26% of the variance ($r^2 = 0.257$). The best model for pears, explained 64% of the variability ($r^2 = 0.637$).

GLM produced for strawberry tree seeds showed that seed weight (Wald $\chi^2 = 29.352$, df = 1, $p < 0.001$) and its interaction with width (Wald $\chi^2 = 26.341$, df = 1, $p < 0.001$) determined the number of days to germination.

Discussion

Our results indicate that in the cork oak woodland area of southwestern Portugal, there are

Table 1. Mean fruit dimensions, size of seed (length, width and weight) collected in the scats or fruits, mean number of seeds per scat and per fruit (± SD) and the consumer species (Gg = *Genetta genetta*, Hi = *Herpestes ichneumon*, Mf = *Martes foina*, Mm = *Meles meles*, Vv = *Vulpes vulpes*).

Fruit				Seeds						Carnivore consumer (no. of seeds/scat)
Length (mm)	Width (mm)	Weight (g)	No. of seeds	Length (mm)		Width (mm)		Weight (g)		
				Fruit	Scat	Fruit	Scat	Fruit	Scat	
Arbutus unedo										
18.73 ± 3.97	20.74 ± 3.75	4.68 ± 2.81	16.78 ± 7.01 (1678)*	2.94 ± 0.51	2.97 ± 0.33	1.54 ± 0.39	1.42 ± 0.19	0.0061 ± 0.040	0.0021 ± 0.008	Gg (12.50 ± 14.27) Hi (44.00 ± 28.28) Mf (15.80 ± 16.35) Mm (34.00 ± 45.25) Vv (5.00 ± 0) Total (289)**
Ficus carica										
32.60 ± 5.64	33.01 ± 3.99	14.45 ± 6.52	563.11 ± 442.24 (19709)*	1.36 ± 0.20	1.46 ± 0.19	1.06 ± 0.20	1.15 ± 0.23	0.0050 ± 0.0004	0.0012 ± 0.0014	Gg (245.93 ± 244.13) Hi (112.00 ± 144.25) Mf (975.00 ± 0) Mm (687.43 ± 1225.42) Vv (412.00 ± 125.87) Total (10288)**
Olea europaea										
18.27 ± 1.62	13.19 ± 1.54	1.87 ± 0.49	1.00 ± 0 (100)*	12.91 ± 1.40	13.43 ± 1.08	6.55 ± 0.57	6.58 ± 0.54	0.3783 ± 0.0862	0.3157 ± 0.0588	Gg (2.27 ± 1.39) Mm (28.73 ± 25.46) Vv (3.67 ± 2.31) Total (997)**
Pyrus bourgaeana										
26.09 ± 10.90	26.07 ± 9.18	13.76 ± 15.74	7.52 ± 2.14 (752)*	6.85 ± 1.52	6.84 ± 0.91	3.65 ± 1.11	4.01 ± 0.90	0.0290 ± 0.0403	0.0331 ± 0.0201	Gg (6.00 ± 6.16) Hi (5.53 ± 5.33) Mf (4.07 ± 3.97) Mm (15.57 ± 10.90) Vv (9.50 ± 3.46) Total (484)**
Rubus sp.										
1.10 ± 0.14	1.26 ± 0.15	0.86 ± 0.27	37.83 ± 9.07 (3783)*	2.47 ± 0.19	2.50 ± 0.37	1.68 ± 0.18	1.66 ± 0.22	0.0017 ± 0.0005	0.0040 ± 0.0062	Gg (37.13 ± 40.31) Hi (117.00 ± 115.97) Mf (439.00 ± 287.09) Mm (15.57 ± 10.90) Vv (18.38 ± 17.00) Total (1697)**
Vitis vinifera										
22.93 ± 2.49	19.46 ± 2.08	5.19 ± 1.41	3.08 ± 1.11 (185)*	5.45 ± 1.55	5.70 ± 0.55	2.88 ± 0.29	3.49 ± 0.34	0.0297 ± 0.0538	0.0246 ± 0.0062	Gg (13.25 ± 12.74) Total (106)**

* total number of planted seeds from fruits, ** total number of planted seeds found in scats.

Table 2. Comparison between the percentage of germinated seeds collected from scat samples (% scat) and seeds isolated from wild fruits (% fruits). χ^2 = Chi-square statistics; – = no consumption; df for all tests = 1. *** = significant at $p < 0.001$.

	% fruits		*Martes foina*	*Meles meles*	*Herpestes ichneumon*	*Genetta genetta*	*Vulpes vulpes*
Arbutus unedo	9.48	% scats	1.45	0	0	0	0
		χ^2	4556.16***	4703.05***	3713.69***	6392.45***	59652.64***
Ficus carica	< 0.001	% scats	0	0	0	< 0.001	0
		χ^2	379.13***	417.07***	1532.60***	86.64***	442.08***
Olea europaea	32.00	% scats	–	41.03	–	41.18	9.09
		χ^2	–	5845.81***	–	59.83***	479.28***
Pyrus bourgaeana	3.72	% scats	1.64	8.42	1.59	4.17	10.53
		χ^2	389.65***	18.48***	379.10***	903.86***	62.43***
Rubus sp.	0.03	% scats	0	0	0	0	0
		χ^2	14.72***	308.59***	41.02***	15.60***	505.33***
Vitis vinifera	0	% scats	–	–	–	0.94	–
		χ^2	–	–	–	1.08***	–

Table 3. Model selection and selected variables incorporated in the best logistic regression models obtained for the data grouping all seed species. Coll_date = collection date, Diet_divers = diet diversity, Au = *Arbutus unedo*, Fc = *Ficus carica*, R = *Rubus* sp., Oe = *Olea europaea*, Vv = *Vitis vinifera*, AIC = Akaike Information Criterion, ΔAIC = difference between AIC values for two nested models, WI = Akaike weight.

Model types	AIC	ΔAIC	WI
1. Fruit_based: Fruit_sp + seed_weight + Coll_date	1545.53	0	0.743
2. Hybrid model: Carnivore_sp + Diet_divers + Fruit_sp + seed_weight + Coll_date	1547.65	2.12	0.257
3. Consumer_based: Carnivore_sp + Diet_divers	1742.31	196.78	< 0.001

Model 1	*B*	SE	*Z*	*p*	Likelihood ratio test (χ^2)	*p*
Fruit*					30.93	< 0.001
Fruit2 (Au)	–0.161	1.041	–0.154	0.877		
Fruit3 (Fc)	0.666	0.643	1.035	0.300		
Fruit4 (R)	–0.129	0.031	–0.042	0.997		
Fruit5 (Oe)	1.307	0.341	3.833	< 0.001		
Fruit6 (Vv)	–2.073	1.021	–2.029	0.042		
Coll_date	0.004	0.0005	8.287	< 0.001	76.33	< 0.001
Weight	3.688	0.993	3.715	< 0.001	269.45	< 0.001
Constant	–3.690	0.223				

* Fruit reference category: *Pyrus bourgaeana*.

Table 4. Model selection and selected variables incorporated in the best logistic regression models obtained for the figs germination data. Coll_date = collection field date, Diet_divers = diet diversity, AIC = Akaike Information Criterion, ΔAIC = difference between AIC values for two nested models, WI = Akaike weight.

Model types	AIC	ΔAIC	WI
1. Simplified consumer_based: Diet_divers	17.07	0	0.737
2. Fruit_based: seed_weight + Coll_date	20.5	3.43	0.166
3. Consumer_based: Carnivore_sp + Diet_divers	21.9	4.83	0.066
4. Hybryd model: Carnivore_sp + Diet_divers + seed_weight + Coll_date	23.4	6.33	0.031

Model 1	*B*	SE	*Z*	*p*	Likelihood ratio test (χ^2)	*p*
Diet_diver	2.771	1.387	–2.333	0.0457	5.277	0.022
Constant	–8.324	3.554				

some carnivore species that seem to promote germination of certain seeds, and thus act as dispersers, while others function as germination inhibitors. While some authors showed contrasting results to this pattern (e.g., Traveset's 1998 review stated that 42% of all non-flying mammals have a neutral effect on seed germination) others stated that mammals could act as important dispersers. In the Sierra de Cazorla (southeastern Spain) for example, almost 40% of the fleshy-fruited plants occurring could be dispersed by mammalian carnivores (Herrera 1989), and in the French Mediterranean region, 32% of all studied plant taxa were dispersed

Table 5. Model selection and selected variables incorporated in the best logistic regression models obtained for the pears germination data. Coll_date = collection field date, Diet_divers = diet diversity, Hi = *Herpestes ichneumon*, Gg = *Genetta genetta*, Mm = *Meles meles*, Vv = *Vulpes vulpes*, AIC = Akaike Information Criterion, ΔAIC = difference between AIC values for two nested models, WI = Akaike weight.

Model types	AIC	ΔAIC	WI
4. Simplified hybrid_based: Carnivore_sp + seed_weight	214.09	0	0.683
3. Hybryd model: Carnivore_sp + Diet_divers+ seed_weight + Coll_date	216.8	2.71	0.253
2. Fruit_based: seed_weight + Coll_date	218.82	4.73	0.064
1. Consumer_based: Carnivore_sp + Diet_divers	234.19	20.01	< 0.001

Model 4	*B*	SE	*Z*	*p*	Likelihood ratio test (χ^2)	*p*
Seed_weight	42.679	9.916	4.304	< 0.001	18.528	< 0.001
Carnivore*					12.271	0.015
Carnivore2 (Hi)	0.926	1.460	0.634	0.526		
Carnivore3(Gg)	2.227	1.496	1.489	0.137		
Carnivore4 (Mm)	2.281	1.066	2.140	0.032		
Carnivore5 (Vv)	2.520	1.081	2.332	0.020		
Constant	–6.394	1.203				

* Carnivore reference category: *Martes foina*.

Table 6. Model selection and selected variables incorporated in the best logistic regression models obtained for the olive germination data. Coll_date = collection field date, Diet_divers = diet diversity, AIC = Akaike Information Criterion, ΔAIC = difference between AIC values for two nested models, WI = Akaike weight.

Model types	AIC	ΔAIC	WI
1. Fruit_based: seed_weight + Coll_date	1272.3	0	0.703
2. Hybryd model: Carnivore_sp + Diet_divers + seed_weight + Coll_date	1275.02	2.72	0.297
3. Consumer_based: Carnivore_sp + Diet_divers	1343.39	71.09	< 0.001

Model 1	*B*	SE	*Z*	*p*	Likelihood ratio test (χ^2)	*p*
Coll_date	0.004	0.001	7.987	< 0.001	63.79	< 0.001
Weight	3.281	0.994	3.301	< 0.001	11.08	< 0.001
Constant	–2.226	0.352				

Table 7. Goodness-of-fit of models.

Models	Percentage of correct classifications	Pearson residuals χ^2-test
All seeds' data	75.4	$\chi^2 = 1589.695$, df = 1617, $p = 0.679$
Figs	88.5	$\chi^2 = 20.762$, df = 25, $p = 0.706$
Pears	93.1	$\chi^2 = 406.262$, df = 463, $p = 0.973$
Olives	63.2	$\chi^2 = 914.766$, df = 906, $p = 0.413$

by mammals, especially the red fox and stone marten (Debussche & Isenmann 1989). Our results showed that the common genet is one of the most effective seed dispersers because of its positive germination effect on pears, olives and grape seeds. This species is a recent invader of Mediterranean Europe (Gaubert *et al.* 2009), where fruits are often available (Herrera 1995), but it behaves more often as a vertebrate predator, especially preying on rodents (Larivière & Calzada 2001, Rosalino & Santos-Reis 2002). Gastrointestinal tracts of most carnivores are relatively short and simple (Stevens & Hume 1998), but the high meat content in carnivore diet typically increases retention time of food in the gut (Silva *et al.* 2005). This increases the time seeds are subjected to mechanical and chemical (gastrointestinal acids and enzymes) abrasion, which can weaken seeds' protection layer (the seed coat) that physically prevents the seedling from growing, and represents a mechanical defence of seeds against predation (Rodgerson 1998). Passage through a predator's gut facilitates a seed coat's split when the embryo grows, thus promoting development when the seed is deposited on the soil together with other faecal organic material (Razanamandranto *et al.* 2004).

Stone martens are an interesting case of a frugivorous carnivore whose role as seed disperser seems to vary throughout its European range. Schaumann and Heinken (2002) concluded that stone martens, as well as pine martens, must be considered important dispersers of the fleshy-fruited plants inhabiting the understory of central European forests. However, Aronne and Russo (1997), and Traveset *et al.* (2001) did not detect any effect of stone martens on seed viability. This species is one of the European southwestern carnivores that include higher proportions of plant biomass (plants and fruits) in their diet (e.g. Posluszny *et al.* 2007, Santos *et al.* 2007). This results in ingested foods passing faster through their guts (Murray *et al.* 1994), thus a neutral effect of ingestion on seed germination could be a results of seeds' spending shorter time in the gut. However, our results seem to point to a deleterious effect on some fruit species, suggesting that additional factors are affecting seed germination viability, and that this species does not function as an effective disperser for Mediterranean fruit species in our study area. This inconsistency of a consumer's role as disperser is not uncommon (*see* Traveset 1998 for other examples), and our results could be a consequence of several interacting factors, whose effects are difficult to untangle: fruit and seed characteristics, which vary geographically and with seed and fruit age (Traveset 1998); constraints on germination imposed by climate unpredictability and the dryness of Mediterranean landscapes (e. g. higher protection from dryness); and type and quality of the food consumed simultaneously with the fruits which can alter the degree of acidity within the gut and in scats, that can affect the seed coat physically and/or chemically (Traveset *et al.* 2001) and consequently decrease its viability.

Foxes and badgers are opportunistic feeders for which fruits and other plant material are important, but vertebrate prey also play an important role in the species trophic ecology (Fedriani *et al.* 1999, Carvalho & Gomes 2004, Santos *et al.* 2007). According to our data, these species have a positive effect on germination and can be considered average seed dispersers among carnivores of southwestern Iberia (which is associated with a moderate digesta speed).

Peco *et al.* (2006) demonstrated that, for Mediterranean grassland plants ingested by sheep (*Ovis* sp.), large-seeded plant species generally had higher survival rates than small-seeded species. Our results seem to support the extrapolation of these inferences towards Mediterranean fleshy-fruits and carnivores. In fact, the heaviest seeds (in our case olives) were those that presented a higher germination rate (reaching 41% for two carnivores dispersers: badgers and genets). Moreover, even within the same species (e.g. pears and olives), seed weight significantly enhanced the germination rate.

Three different weight-related factors probably act synergistically in promoting seed survival. Heavier seeds can be the result of a thicker seed coat, a greater supply of nutrients for the embryo, or a larger embryo (although embryo size is thought to be less important than the other factors). A thicker seed coat gives more efficient protection (Razanamandranto *et al.* 2004), while a larger nutrient supply can help the embryo's survival for longer periods in a disperser's digestive track. There is also an evidence that longer periods inside the digestive tract, with the consequent higher mechanical and chemical abrasions, seem to enhance germination after dormancy is interrupted (Traveset 1998, Schaumann & Heinken 2002). Moreover, a higher amount of nutrient (endosperm) means that structurally the embryo is located more internally (Baskin & Baskin 1998), which helps to prevent embryonic damage caused by external factors, since the lower surface/volume ratio could decrease the impact of acids and digestive fluids (Peco *et al*. 2006).

The consumption of olives later in the season, which significantly promotes their germination, could be associated with weakening of the seed's protective layer. Olives have a slow decay rate (Kruuk & De Kock 1981), and after falling from trees they are still available to carnivores (e.g. badgers, *see* Loureiro 2008). However, during this period, when they are on the soil surface or semi-buried, the seeds' protective layer is subject to external stressors that weaken their resistance (e.g. humidity, rain, bacteria, fungi, insects, etc.). These factors, together with the mechanical and chemical aggression of dispersers' gut probably facilitate splitting of the seed coat to allow germination.

Although an increase in fig germination is low, our model showed that for figs, germination of ingested seeds is promoted by increased number of prey types in a meal. Removal of drupelets (small parts of an aggregate fruit) from the syconium (the fleshy part of the fig, containing the drupelets), when they are eaten by carnivores, aids germination since it eliminates the effect of inhibitors and/or microenvironments with high osmotic pressure inside the syconium (Lisci & Pacini 1994). Moreover, although we are still uncertain what could be causing the reported germination pattern, we believe that it could be related to the nutrient needs of drupelet embryos, which are satisifed when seeds are excreted with highly diverse mineral material composing non-digested excreta.

The germination period (defined here as the number of days between planting and emergence of the seedling at the soil surface) was further influenced by the morphological characteristics of the seeds. Morphology acts as the main factor promoting germination in some cases (seed width in figs and weight in strawberry tree fruits) or in combination with other variables, as detected in pears.

Frequently there is a positive correlation between seed mass and survival and growth (e.g. Bonfil 1998). Therefore, although heavier seeds are more prone to germinate, among those that do germinate, the smallest need less time to develop. This might be related to the nutrient reserves available to the embryo. Heavier seeds have more reserves and thus embryos can delay their germination without compromising seed viability. Inversely, smaller seeds, if surviving the disperser gut, must germinate sooner because of scarce nutrient reserves. Moreover, early germinated smaller seeds have an advantage of accessing a larger share of resources (water, light and other nutrients), or even allowing the seedling to take advantage of a growth period before the severe summer drought, typical for southern mediterranean landscapes (Traba *et al*. 2006).

An important consequence of the ingestion, and consequent dispersal, of cultivated fruits (e.g., olives, grapes and figs in our study) is its deleterious effects on natural or regenerating landscapes through introduction of these agrarian species into the species pool (Matías *et al*. 2010). Although it can represent almost a negligible fraction of the consumed fruits in some areas (e.g. only 0.14% in a study implemented in Sierra de Cazorla, southeastern Spain, *see* Herrera 1989), in our study they reach 50%, and could be an important factor to take into consideration. This dispersion affects particularly regenerating habitats, where species richness is lower and germination opportunities for cultivated species higher and where mammals can act as long-distance dispersal vectors (*see* e.g. Matías *et al*. 2010). However, our study area is composed of a landscape shaped by centuries of human activities (cork oak woodland or "montado"), characterized by a multi-use system traditional in rural landscapes of southern Europe, where agricultural, silvicultural, and pastoral production are combined to provide a sustainable use of natural and human resources (Makhzoumi 1997). In this landscape, orchards and olive yards have been a part of the system for centuries, and are particularly important in terms of vertebrate conservation, because of the diverse wildlife that they support (Diáz *et al*.

1997), and therefore the non-native dispersion in the community is minor.

Although our results contribute to a better understanding of the role of carnivores in the effective dispersion of Mediterranean fleshy fruits, it is important to reinforce the idea that the effect of dispersers on seed germination is not universal and varies with plant species, fruit type, retention time of seeds in the disperser's gut, environmental conditions and geographical location (Razanamandranto *et al*. 2004). However, this data highlights the role of many carnivores inhabiting a Mediterranean region of southwestern Europe as potential seed dispersers, by identifying fruits consumed by those species and assessing their effect on seed germination. The importance of carnivores as dispersers is enhanced by the fact that seed dispersal is considered a major vector of gene flow among remnant patches of natural vegetation (Bacles *et al*. 2006).

Acknowledgements

The study was funded by the Fundação para a Ciência e a Tecnologia and FEDER (POCI 2010) (POCI-PPCDT/BIA-BDE-61122/2004) and LMR Postdoctoral fellowship: SFRH/BPD/14435/2003). Special thanks are due to João do Rosário for helping in the field work, Teresa Sales-Luís and Mafalda Basto for the assistance in the seeds experiment, and Elizabeth Chadwick for the English revision of the manuscript. We declare that the experiments comply with the Portuguese current laws.

References

Aronne, G. & Russo, D. 1997: Carnivorous mammals as seed dispersers of *Myrtus communis* (Myrtaceae) in the Mediterranean shrublands. — *Plant Biosystems* 131: 189–195.

Bacles, C. F. E., Lowe, A. J. & Ennos, R. A. 2006: Effective seed dispersal across a fragmented landscape. — *Science* 311: 628.

Baskin, C. & Baskin, J. 1998: *Seeds: ecology, biogeography, and evolution of dormancy and germination*. — Academic Press, San Diego.

Bonfil, C. 1998: The effect of seed size, cotyledon reserves, and herbivory on seedling survival and growth in *Quercus rugosa* and *Q. laurina* (Fagaceae). — *American Journal of Botany* 85: 79–87.

Carvalho, J. C. & Gomes, P. 2004: Feeding resource partitioning among four sympatric carnivores in the Peneda-Gerês National Park (Portugal). — *Journal of Zoology, London* 263: 275–283.

Correia, A. I. & Santos-Reis, M. 1999: Área de estudo. — In: Santos-Reis, M. & Correia, A. I. (eds.), *Caracterização da flora e da fauna do montado da Herdade da Ribeira Abaixo (Grândola — Baixo Alentejo)*: 5–8. Centro de Biologia Ambiental.

Corlett, R. T. 1995: Tropical secondary forests. — *Progress in Physical Geography* 19: 159–172.

Corlett, R. T. 1998: Frugivory and seed dispersal by vertebrates in the oriental (Indomalayan) region. — *Biological Reviews* 73: 413–448.

Debussche, M. & Isenmann, P. 1989: Fleshy fruits characters and the choices of birds and mammal seed dispersers in a Mediterranean region. — *Oikos* 56: 327–338.

Diáz, M., Campos, P. & Pulido, F. J. 1997: The Spanish dehesas: a diversity in land-use and wildlife. — In: Pain, D. J. & Pienkowski, M. W. (eds.), *Farming and birds in Europe: the common agricultural policy and its implication for birds conservation*: 178–209. Academic Press, London.

Fedriani, J. M., Palomares, F. & Delibes, M. 1999: Niche relations among three sympatric Mediterranean carnivores. — *Oecologia* 121: 138–148.

Gaubert, P., Godoy, J. A., Cerro, I. & Palomares, F. 2009: Early phases of a successful invasion: mitochondrial phylogeography of the common genet (*Genetta genetta*) within the Mediterranean Basin. — *Biological Invasion*s 11: 523–546.

Herrera, C. M. 1995: Plant–vertebrate seed dispersal system in the Mediterranean: ecological, evolutionary, and historical determinants. — *Annual Review of Ecology and Systematic* 26: 705–727.

Herrera, C. M. 1989: Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. — *Oikos* 55: 250–262.

Hosmer, D. W. & Lemeshow, S. 2002: *Applied logistic regression*. — John Wiley & Sons, Inc, New York.

Jordano, P., García, C., Godoy, J. A. & García-Castaño, J. L. 2007: Differential contribution of frugivores to complex seed dispersal patterns. — *PNAS* 104: 3278-3282.

Kruuk, H. & de Kock, L. 1981: Food and habitat of badgers (*Meles meles* L.) on Monte Baldo, northern Italy. — *Zeitschrift für Säugetierkunde* 46: 295–301.

Larivière, S. & Calzada, J. 2001: *Genetta genetta*. — *Mammalian Species* 680: 1–6.

Lisci, M. & Pacini, E. 1994: Germination ecology of drupelets of the fig (*Ficus carica* L.). — *Botanical Journal of the Linnean Society* 114: 133–146.

Loureiro, C. F. M. 2008: *Time and space use of key resources by the Eurasian badger (Meles meles) in a Mediterranean cork oak woodland: conservation implications*. — Ph.D. thesis, Universidade de Lisboa, Lisboa.

Macdonald, D. W. & Barrett, P. 1993: *Mammals of Britain and Europe*. — Harper Collins Publishers, London.

Makhzoumi, J. M. 1997: The changing role of rural landscapes: olive and crob multi-use tree plantations in the semiarid Mediterranean. — *Landscape and Urban Planning* 37: 115–122.

Maroco, J. 2007: *Análise estatística com utilização do SPSS*.

— Edições Sílabo, Lisboa.

Matías, L., Zamora, R., Mendoza, I. & Hódar, J. A. 2010: Seed dispersal patterns by large frugivorous mammals in a degraded mosaic landscape. — *Restoration Ecology*. [In press].

Matos, H. M., Santos, M. J., Palomares, F. & Santos-Reis, M. 2009: Does riparian habitat condition influence mammalian carnivore abundance in Mediterranean ecosystems? — *Biodiversity and Conservation* 18: 373–386.

Moreno, R. S., Kays, R. W. & Samudio, R. 2006: Competitive release in diets of ocelot (*Leopardus pardiolis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. — *Journal of Mammalogy* 87: 808–816.

Murray, K. G., Russell, S., Picone, C. M., Winnett-Murray, K., Sherwood, W. & Kuhlmann, M. L. 1994: Fruit laxatives and seed passage rates in frugivores: consequences for plant reproductive success. — *Ecology* 75: 989–994.

Nathan, R., Schurr, F. M., Spiegel, O., Steinitz, O., Trakhtenbrot, A. & Tsoar, A. 2008: Mechanisms of long-distance seed dispersal. — *Trends in Ecology and Evolution* 23: 638–647.

Peco, B., Lopez-Merino, L. & Alvir, M. 2006: Survival and germination of Mediterranean grassland species after simulated sheep ingestion: ecological correlates with seed traits. — *Acta Oecologica* 30: 269–275.

Pigozzi, G. 1992: Frugifory and seed dispersal by the European badger in a Mediterranean habitat. — *Journal of Mammalogy* 73: 630–639.

Posluszny, M., Pilot, M., Goszczynski, J. & Gralak, B. 2007: Diet of sympatric pine marten (*Martes martes*) and stone martes (*Martes foina*) identified by genotyping of DNA from faeces. — *Annales Zoologici Fennici* 44: 269–284.

Razanamandranto, S., Tigabu, M., Neya, S. & Odén, P. C. 2004: Effects of gut treatment on recovery and germinability of bovine and ovine ingested seeds of four woody species from the Sudanian savanna in West Africa. — *Flora* 199: 389–397.

Reynolds, J. C. & Aebischer, N. J. 1991: Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. — *Mammal Review* 21: 97–122.

Rodgerson. L. 1998: Mechanical defence in seeds adapted for ant dispersal. — *Ecology* 79: 1669–1677.

Rosalino, L. M. & Santos-Reis, M. 2002: Feeding habits of the common genet *Genetta genetta* (Carnivora: Viverridae) in a semi-natural landscape of Central Portugal. — *Mammalia* 66: 195–205.

Rosalino, L. M. & Santos-Reis, M. 2009: Fruit consumption by carnivores in Mediterranean Europe. — *Mammal Review* 39: 67–78.

Rosalino, L. M., Loureiro, F., Macdonald, D. W. & Santos-Reis, M. 2005: Dietary shifts of the badger (*Meles meles*) in Mediterranean woodlands: an opportunistic forager with seasonal specialisms. — *Mammalian Biology* 70: 12–23.

Santos, M. J., Pinto, B. M. & Santos-Reis, M. 2007: Trophic niche partitioning between two native and two exotic carnivores in SW Portugal. — *Web Ecology* 7: 53–62.

Santos, M. J., Pedroso, N. M., Ferreira, J. P., Matos, H. M., Sales-Luís, T., Pereira, I., Baltazar, C., Grilo, C., Cândido, A. T., Sousa, I. & Santos-Reis, M. 2008: Assessing dam implementation impact on threatened carnivores: the case of Alqueva in SE Portugal. — *Environmental Monitoring and Assessment* 142: 47–64.

Santos-Reis, M., Rosalino, L. M. & Rodrigues, M. 1999: Lagomorfos, Carnívoros e Artiodáctilos (Mamíferos). — In: Santos-Reis, M. & Correia, A. I. (eds.), *Caracterização da flora e da fauna do montado da Herdade da Ribeira Abaixo (Grândola — Baixo Alentejo)*: 249–262. Centro de Biologia Ambiental.

Schaumann, F. & Heinken, T. 2002: Endozoochorous seed dispersal by martens (*Martes foina*, *M. martes*) in two woodland habitats. — *Flora* 197: 370–378.

Shanahan, M., So, S., Compton, S. G. & Corlett, R. 2001: Fig-eating by vertebrate frugivores: a global review. — *Biological Reviews* 76: 529–572.

Silva, S. I., Jaksic, F. M. & Bozinovic, F. 2005: Nutritional ecology and digestive response to dietary shift in the large South American fox, *Pseudalopex culpaeus*. — *Revista Chilena de Historia Natural* 78: 239–246.

Simpson, G. G., Roe, A. & Lewontin, R. C. 1960: *Quantitative zoology*. — Harcourt, Brace and Company Inc., New York.

Stevens, C. E. & Hume, I. D. 1998: Contributions of microbes in vertebrate gastrointestinal tract to production and conservation of nutrients. — *Physiological Reviews* 78: 393–427.

Tabachnick, B. G. & Fidell, L. S. 1996: *Using multivariate statistics*. — Harper Collins College Publishers, New York.

Traba, J., Sagrario, A., Jesús, H. & Cristina, C. M. 2006: Red fox (*Vulpes vulpes* L.) favour seed dispersal, germination and seedling survival of Mediterranean Hackberry (*Celtis australis* L.). — *Acta Oecologica* 30: 39-45.

Traveset, A. 1998: Effect of seed passage through vertebrate frugivores' guts on germination: a review. — *Perspectives in Plant Ecology, Evolution and Systematics* 1: 151–190.

Traveset, A., Riera, N. & Mas, R. E. 2001: Ecology of fruit-colour polymorphism in *Myrtus communis* and differential effects of birds and mammals on seed germination and seedling growth. — *Journal of Ecology* 89: 749–760.

Verdú, M. & Traveset, A. 2004: Bridging meta-analysis and the comparative method: a test of seed size effect on germination after frugivores' gut passage. — *Oecologia* 138: 414–418.

Virgós, E., Tellería, J. L. & Santos, T. 2002: A comparison on the response to forest fragmentation by medium-sized Iberian carnivores in central Spain. — *Biodiversity and Conservation* 11: 1063–1079.

Zuur, A. F., Ieno, E. N. & Smith, G. M. 2007: *Analysing ecological data*. — Springer, New York.

Zar, J. H. 1999: *Biostatistical analysis*. — Prentice Hall, Inc., New Jersey.