

Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats

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The role of carnivorous mammals (Order Carnivora) in seed dispersal has remained virtually unexplored, despite the well-known fact that these animals commonly ingest fleshy fruits and defecate their seeds. This paper presents data on the dispersal of seeds by carnivores in an extensive area of relatively undisturbed habitats in south-eastern Spain, and is based on the examination of more than 1,500 carnivore feces collected over a 10-yr period. Seeds from 27 plant species, representing 40% of the fleshy-fruited plants occurring in the region, were recovered from carnivore feces. Carnivores actually disperse the seeds of the vast majority of eaten fruits, as only 0.89% of the seeds found were visibly damaged (broken or cracked). Fruits eaten by carnivores represent a nonrandom subset of the regional flora with regard to color, scent, persistence after ripening, size, seediness, relative pulp richness, chemical composition of the pulp (protein, fiber, minerals), and plant growth form. Carnivore eaten species are also dispersed by birds, thus displaying a dual seed dispersal system, while species not eaten by carnivores are entirely bird-dispersed. Consideration of mammalian carnivores seems essential for a complete understanding of seed dispersal processes in the broad assemblage of Mediterranean plants having mixed, bird-mammal dispersal. Available evidence suggests that fruit features associated with carnivore consumption correspond to a “generalized mammalian syndrome”, and that carnivore dispersal represents the vanishing remnants of a more complex pre-Holocene plant-mammal seed dispersal system.

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Introduction

Considerable information has accumulated in recent years on the ecology of frugivory and seed dispersal by vertebrates in temperate and tropical habitats (Estrada and Fleming 1986, Howe 1986, Willson 1986, and references therein). While seed dispersal by birds has attracted the most attention, the role of reptiles (e.g., Hnatiuk 1978, Braun and Brooks 1987, Whitaker 1987) and mammals as plant dispersal agents has also been examined frequently. Studies of frugivory and seed dispersal by mammals have traditionally focused on monkeys (e.g., Howe 1980, Gautier-Hion 1984, Estrada and Coates-Estrada 1984, Garber 1986) and bats (e.g.,

Fleming 1981, 1986, Heithaus 1982), two groups whose importance as seed vectors had long been recognized (Ridley 1930, van der Pijl 1957). The significance of large herbivorous mammals in seed dispersal has also been documented in detail in recent years (e.g., Alexandre 1978, Janzen 1981a,b, 1982, 1984). In contrast, the role of carnivorous mammals (Order Carnivora; throughout this paper, the adjective “carnivorous” is used in its taxonomic sense) in seed dispersal remains virtually unexplored, having received only anecdotal consideration in recent studies (Bonaccorso et al. 1980, Stiles 1980, Bullock 1981, Leighton and Leighton 1983, Rogers and Applegate 1983, Estrada et al. 1984, Pannell and Koziol 1987). Seed dispersal by carnivores is

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not even considered explicitly in some recent reviews (Janzen 1983, Howe 1986, Renner 1987), thus denoting a scarcity of primary literature on the subject (but see González-Espinosa and Quintana-Ascencio 1986, Janzen 1986).

The neglect of carnivores as the subject of studies on seed dispersal is curious since it is well-known that many species of carnivorous mammals routinely ingest large quantities of fleshy fruits (e.g., Corbet and Southern 1977, Halls 1977, Chapman and Feldhamer 1982, Smythe 1986). Furthermore, Ridley (1930), who presented data on seed dispersal by a variety of species in the Felidae, Ursidae, Viverridae, Canidae and Mustelidae, noted long ago that carnivorous mammals often behave as legitimate seed dispersers. Van der Pijl (1982), however, did not pay particular attention to the dispersal of seeds by carnivores because "in northern regions so few original mammalian dispersers survive, and so many edible fruits are introductions, that it is difficult to reconstruct the original relations." Here may lie one of the reasons for the neglect noted above. The scarcity of extensive natural habitats and the disappearance of carnivore populations in temperate latitudes probably are responsible, in part, for our present ignorance about the role of these vertebrates in the dispersal of seeds in natural habitats. A further likely reason is the inherent difficulty of collecting data or observations on carnivores' frugivory, due to their foraging habits and low population densities.

In this paper, I present data collected over a 10-yr period on the dispersal of seeds by three species of carnivores in an extensive area of relatively undisturbed habitats in southeastern Spain. Results indicate that, in the Mediterranean Basin, carnivores probably played a major role in seed dispersal before extensive habitat deterioration, and that plants whose fruits are eaten (and seeds dispersed) by carnivores represent a distinct subset of the regional fleshy-fruited flora with regard to fruit characteristics.

Study area and methods

The study was carried out in the Reserva de Navahondona-Guadahornillos, located in the Sierra de Cazorla (Jaén province, southeastern Spain). The Reserva, which includes a variety of habitat types, has an extension of over 20,000 ha, and elevation ranges between 700–2000 m. Descriptions of the vegetation of the area may be found in Fernández Galiano and Heywood (1960), Polunin and Smythies (1973: 83–89), J. Herrera (1984) and Valle (1985). The degree of conservation of the natural vegetation varies from virtually undisturbed to lightly disturbed forests. The latter occur in areas surrounding long-abandoned, small human settlements, or where recent silvicultural practices have managed the forest to favor valuable timber trees. The area is also one of the few enclaves in southern Spain with a diverse and comparatively unaltered (in recent times) verte-

brate fauna, although three species of mammals have become extinct in historical times (*Ursus arctos*, *Canis lupus* and *Capreolus capreolus*; J. A. Valverde, pers. comm.). Eight species of carnivores still occur in the region (Otero et al. 1978).

Six large areas within the Reserva were chosen for this study, based on habitat type, degree of disturbance, and accessibility. (A) The lower portion of the Arroyo de las Truchas valley, ranging in elevation between 700–1100 m. The vegetation is undisturbed Mediterranean evergreen forest with *Quercus rotundifolia*, *Q. faginea*, *Arbutus unedo*, and *Phillyrea latifolia* as dominant tree species. (B) The upper portion of the same valley, with an elevational range of 1100–1400 m. The vegetation is undisturbed mixed forest, and *Q. rotundifolia*, *Q. faginea*, *Juniperus oxycedrus* and *Pinus nigra* are the dominant trees. (C) The highlands extending between Puente de Guadahornillos and Fuente de la Umbría, elevation 1400–1800 m. The vegetation is undisturbed *Pinus nigra* woodland with a sparse undergrowth dominated by *Juniperus communis*, *J. phoenicea* and rosaceous trees and shrubs. J. Herrera (1984) presents a detailed description of the vegetation of areas A, B and C. (D) A portion of the Guadalquivir River valley, between El Calerón and Los Rasos, and the adjacent Arroyo de Los Habares valley, elevation 1100–1300 m. Lightly disturbed *P. nigra*-*Q. rotundifolia* mixed forest with cleared undergrowth. (E) The highlands of Nava Noguera, Nava de Pablo and Torcal del Cerecino (elevation 1400–1800 m). The vegetation is selectively logged *P. nigra* woodland with successional patches in areas where the undergrowth has been cleared. (F) The uppermost portion of the Guadalquivir River valley and contiguous areas between Cañada de las Fuentes and Pino de Las Cruces (1300–1700 m elevation). Selectively logged *P. nigra* forest with cleared undergrowth and young pine plantations.

Depending on availability of paths, one or several routes, totalling at least 2.5 km, were chosen in each area. From April 1983 through March 1988, most routes were walked at least every two months in search of carnivore feces (see below). Nevertheless, as snow cover often precluded access to highland areas in winter and early spring, and persistent rains (which washed away feces) on the days preceding sampling dates sometimes precluded feces collection, important differences between areas in sampling effort accumulated over the years. For this reason, no attempt is made in this paper at performing any analysis requiring strict homogeneity of sampling effort among areas. A comparatively small number (N = 169) of carnivore feces collected casually during 1978–1982 in the same areas have been included in the analyses, on the basis that no homogeneity of sampling effort between areas will be assumed.

All fresh carnivore feces found while walking the predetermined routes were examined in situ for seeds or fruit remains. Those without any sign of fruit remains were discarded, and doubtful and fruit-containing ones

Tab. 1. Frequency of occurrence (%) of seed species in carnivore feces collected from several habitats of the Sierra de Cazorla, southeastern Spain. Figures in bold type indicate the species occurring most frequently at a given area and season (summed frequencies of occurrences > 75%). Areas A-F are described in the text.

	Virtually undisturbed habitats											
	Area A Mediterranean forest (700-1100 m)				Area B Mixed forest (1100-1400 m)				Area C Coniferous forest (1400-1800 m)			
	Jun- Aug 29	Sep- Nov 230	Dec- Feb 89	Mar- May 25	Jun- Aug 38	Sep- Nov 252	Dec- Feb 176	Mar- May 62	Jun- Aug 66	Sep- Nov 66	Dec- Feb 37	Mar- May 7
Number of samples												
<i>Amelanchier ovalis</i> (Rosaceae)	3.5	0.4	.	.	5.3	.	.	.	6.1	1.5	.	.
<i>Arbutus unedo</i> (Ericaceae)	.	3.0	31.5	8.0	.	1.2	14.8	6.5	.	.	2.7	.
<i>Crataegus laciniata</i> (Rosaceae)	.	0.4	2.3	8.0	.	0.4	1.7	1.6	.	9.1	8.1	.
<i>Crataegus monogyna</i> (Rosaceae)	.	0.4	.	.	.	1.2	.	3.2	.	12.1	2.7	.
<i>Ficus carica</i> (Moraceae)	.	27.8	3.4	8.0	2.6	26.2	7.4	.	.	18.2	2.7	.
<i>Juniperus communis</i> (Cupressaceae)	2.6	1.5	.	.
<i>Juniperus oxycedrus</i> (Cupressaceae)	.	2.2	33.7	36.0	5.3	17.9	65.3	72.6	.	7.6	64.9	71.4
<i>Juniperus phoenicea</i> (Cupressaceae)	89.7	13.9	15.7	48.0	65.8	7.1	16.5	14.5	3.0	1.5	2.7	.
<i>Juniperus sabina</i> (Cupressaceae)	0.4	.	1.6	.	.	2.7	.
<i>Malus sylvestris</i> (Rosaceae)	.	0.4	1.6	.	1.5	.	.
<i>Olea europaea</i> (Oleaceae)	.	0.4	0.5	.	.
<i>Pistacia terebinthus</i> (Anacardiaceae)	.	4.5	.	.	.	2.0	2.8	.	.	6.1	.	.
<i>Prunus avium</i> (Rosaceae)	3.5	1.5	.	.	.
<i>Prunus domestica</i> (Rosaceae)	.	7.0	.	.	10.5	0.8	.	.	6.1	7.6	.	.
<i>Prunus mahaleb</i> (Rosaceae)	15.8	.	.	.	86.4	12.1	.	.
<i>Pyrus</i> sp. (Rosaceae)	.	0.4
<i>Rosa canina</i> (Rosaceae)	.	.	3.4	.	.	11.1	9.7	16.1	1.5	22.7	37.8	57.1
<i>Rubus ulmifolius</i> (Rosaceae)	3.5	63.9	4.5	8.0	.	65.9	2.8	1.6	.	37.9	2.7	.
<i>Sorbus aria</i> (Rosaceae)	.	0.4	3.4	.	.	0.4	2.8	.	.	7.6	.	.
<i>Sorbus domestica</i> (Rosaceae)	3.5	32.6	31.5	12.0	.	22.6	6.8	1.6	.	10.6	.	.
<i>Sorbus torminalis</i> (Rosaceae)	.	8.7	7.9	.	.	7.9	1.1	.	.	.	2.7	.
<i>Taxus baccata</i> (Taxaceae)	2.8	.	.	.	3.0	.	.
<i>Viscum album</i> (Loranthaceae)	1.6	1.5	.	2.7	.
<i>Vitis vinifera</i> (Vitaceae)	3.5	3.5	2.3	.	.	0.8	.	.	.	3.0	.	.
Number of species/period	6	17	11	7	7	16	11	11	7	18	11	2
Number of species/area			19				21				23	

were collected, air dried, and stored individually in paper bags. Feces collected were from red fox (*Vulpes vulpes*), badger (*Meles meles*) and stone marten (*Martes foina*). I could not confidently separate all collected feces as to mammal species, so they have been combined into a single sample for the analyses, since the aim of this paper is to examine seed dispersal and frugivory by carnivores in a general fashion. Feces from the three species above occurred in all the areas sampled.

Before examination, feces were held for 1-1.5 months in individual plastic containers in a water solution of concentrated detergent (1:1). After this period, each one was thoroughly washed under running water on a sieve (0.25 mm mesh size) and air dried. Upon examination, the percentage in volume made up by animal remains was estimated visually, and the number of seeds present was counted and identified to species. Particular care was taken to detect any remain of seed coat that would denote the presence of broken seeds. When remains of seed coats were present, I estimated the number of entire seeds that would best account for

them. Separate records were kept for intact and broken (estimated from seed coat remains) plus cracked seeds ("damaged seeds" hereafter). As used here, figures for "damaged seeds" provide conservative estimates of seed damage, as seed viability may be impaired even if no cracking or breakage occur.

One objective of this paper is to identify the possible correlates of fruit consumption by carnivorous mammals. The complete list of fleshy-fruited species occurring in the area was compiled (based on my 10-yr field experience there), and fruit characteristics gathered for each species. The species list was then divided into two groups, eaten and not eaten by carnivores, and between-group comparisons of fruit characteristics performed. Data on ripe fruit characteristics (structure, color, pulp chemical composition) were taken from Herrera (1987: Tab. A1, A2), and detailed presentation of these data is omitted.

Further characteristics considered here are scent and persistence on the plant of the ripe fruits. I scored species for detectable (to the human nose) scent of the

Tab. 1, extended

Number of samples	Lightly disturbed habitats								
	Area D Mixed forest (1100-1300 m)		Area E Coniferous forest (1400-1800 m)				Area F Coniferous forest (1300-1700 m)		
	Sep- Nov 50	Dec- Feb 69	Jun- Aug 111	Sep- Nov 34	Dec- Feb 53	Mar- May 4	Jun- Aug 25	Sep- Nov 80	Dec- Feb 32
<i>Amelanchier ovalis</i> (Rosaceae)	.	.	0.9	.	.	.	4.0	.	.
<i>Arbutus unedo</i> (Ericaceae)
<i>Crataegus laciniata</i> (Rosaceae)	1.9
<i>Crataegus monogyna</i> (Rosaceae)	.	.	.	26.5	20.8	.	.	11.3	6.3
<i>Ficus carica</i> (Moraceae)	4.0	2.9	0.9	.	.	.	4.0	5.0	6.3
<i>Juniperus communis</i> (Cupressaceae)
<i>Juniperus oxycedrus</i> (Cupressaceae)	22.0	75.4	.	2.9	15.1	.	.	5.0	3.1
<i>Juniperus phoenicea</i> (Cupressaceae)	6.0	.	0.9	8.8	1.9	.	.	2.5	6.2
<i>Juniperus sabina</i> (Cupressaceae)	.	4.4	.	.	3.8
<i>Malus sylvestris</i> (Rosaceae)	.	1.5	0.9	1.3	.
<i>Olea europaea</i> (Oleaceae)
<i>Pistacia terebinthus</i> (Anacardiaceae)	34.0	10.0	3.1
<i>Prunus avium</i> (Rosaceae)	2.0	.	2.7	.	.	.	4.0	.	.
<i>Prunus domestica</i> (Rosaceae)	8.0	.	1.8	.	.	.	16.0	2.5	.
<i>Prunus mahaleb</i> (Rosaceae)	.	.	96.4	23.5	.	.	76.0	8.8	.
<i>Pyrus</i> sp. (Rosaceae)	4.0	.	.
<i>Rosa canina</i> (Rosaceae)	2.0	4.4	.	50.0	73.6	100.0	.	42.5	12.5
<i>Rubus ulmifolius</i> (Rosaceae)	68.0	.	.	8.8	.	.	4.0	23.8	.
<i>Sorbus aria</i> (Rosaceae)	.	.	.	8.8	7.6	.	.	15.0	.
<i>Sorbus domestica</i> (Rosaceae)	3.1
<i>Sorbus torminalis</i> (Rosaceae)	1.3	.
<i>Taxus baccata</i> (Taxaceae)	4.0
<i>Viscum album</i> (Loranthaceae)	.	39.1	.	9.4	.	.	.	18.8	71.9
<i>Vitis vinifera</i> (Vitaceae)	.	.	.	2.9	.	.	.	1.3	3.1
Number of species/period	9	6	7	9	7	1	7	14	9
Number of species/area		12			16			18	

ripe fruit. Determining whether a ripe fruit is scented is subjective. To check my assignments, a questionnaire was submitted independently to two persons having extensive field experience with fleshy fruits in the area, asking them to score fruit species in the regional list for presence or absence of scent in the ripe fruit. Their scores and mine were subjected to Cochran Q-test for matched samples (Siegel 1956), and no significant interindividual differences were found ($P > 0.05$). Assignments to scent classes used in this paper thus actually reflect consistent interspecific differences from the viewpoint of humans. Fruits were considered persistent on the plants if at least an estimated 90% of fruits do not fall naturally to the ground within the three weeks after ripening. Assignment of species to persistence classes (persistent vs non-persistent) were made on the basis of previous studies (C. M. Herrera 1984a, Obeso 1986) and personal observations. It must be noted that, despite broad interspecific differences in degree of fruit persistence within the "non-persistent fruit" species set, plant species in the study region fall clearly into one of

the two categories considered. The complete regional plant species list, along with the fruit scent and persistence data used, are presented in the Appendix.

Throughout this paper, means are presented ± 1 SD, and N denotes sample size.

Results

Occurrence of seeds

Seeds from at least 27 plant species were recovered from the carnivore feces examined (Tab. 1; *Berberis hispanica*, *Daphne gnidium* and *Phillyrea latifolia*, each contributing single seed occurrences, were omitted from the table). At least 6 *Rosa* species are found in the region (Fernández Galiano and Heywood 1960), but I was unable to separate their seeds by species; they are lumped here under *R. canina*, which is the most abundant species of its genus in the region. All seeds reco-

Tab. 2. Proportion of damaged (broken plus cracked) seeds and number of seeds per fecal sample, in feces from carnivorous mammals, all sites and seasons combined. Species totalling less than 50 seeds have been omitted. Proportion of damaged seeds could not be estimated for the two species marked with asterisks; figures for these species were excluded from the computation of percent damage for all species combined.

Plant species	Total seeds recovered	Fraction damaged (%)	Seeds/fecal sample			
			N	Mean	(SD)	Median
<i>Amelanchier ovalis</i>	587	2.04	11	53.4	(69.2)	22
<i>Arbutus unedo</i> *	5,251	—	71	74.0	(120.9)	18
<i>Crataegus laciniata</i>	306	0.	20	15.3	(13.6)	8
<i>Crataegus monogyna</i>	798	1.63	46	17.3	(17.8)	11
<i>Ficus carica</i> *	61,685	—	174	354.5	(526.4)	177
<i>Juniperus communis</i>	80	37.50	2	40.0	(38.0)	40
<i>J. oxycedrus</i>	8,297	1.59	362	22.9	(26.0)	15
<i>J. phoenicea</i>	14,264	0.09	181	78.8	(73.9)	61
<i>J. sabina</i>	70	14.29	8	8.8	(7.9)	7
<i>Pistacia terebinthus</i>	338	98.52	51	6.6	(8.3)	3
<i>Prunus avium</i>	89	3.37	7	12.7	(13.9)	7
<i>P. domestica</i>	221	0.45	43	5.1	(5.7)	3
<i>P. mahaleb</i>	15,782	2.62	212	74.4	(60.3)	57
<i>Rosa canina</i>	9,317	0.09	194	48.0	(69.2)	21
<i>Rubus ulmifolius</i>	94,112	0.29	409	230.1	(253.6)	168
<i>Sorbus aria</i>	231	8.23	34	6.8	(6.5)	5
<i>S. domestica</i>	743	2.56	185	4.0	(3.7)	3
<i>S. torminalis</i>	556	5.22	51	10.9	(12.4)	6
<i>Taxus baccata</i>	178	0.	11	16.2	(14.3)	17
<i>Viscum album</i>	2,090	0.	73	28.6	(23.7)	22
<i>Vitis vinifera</i>	108	0.	18	6.0	(6.8)	3
All species combined	215,103	0.89	1,535	140.2	(261.4)	49

vered were from fleshy-fruited plants producing berries, drupes, or functionally analogous fruits (e.g., fleshy cones of gymnosperms). With minor exceptions, all seeds were from wild native plants (99.86% of a total of 215,103 seeds recovered). Exceptions were *Olea europaea*, which does not occur naturally in the area but is widely cultivated a few kilometers away, and *Prunus domestica* and *P. avium*, which have scattered feral populations in favourable habitats and have become naturalized after escaping from cultivation. Seeds most frequently found were from *Juniperus oxycedrus*, *J. phoenicea*, *Rubus ulmifolius*, *Rosa canina* and *Prunus mahaleb*. There were, however, distinct seasonal and between-habitat variations.

In June–August, the seeds recorded most frequently in carnivore feces were those of *P. mahaleb* (in highland pine forests) and *J. phoenicea* (in Mediterranean and mixed forests). In the period September–November, *R. ulmifolius* was the most frequent species in feces from all habitat types except the two areas of lightly disturbed highland forest, where *R. canina* seeds occurred most often. During December–February, *J. oxycedrus* was the commonest species in all the areas except in disturbed highland forests, where *R. canina* and *Viscum album* fruits occurred most frequently. Finally, the period March–May was characterized by the dominance of either *J. oxycedrus* or *J. phoenicea* in all the areas with sufficient samples. The scarcity of samples from the spring period corresponds in part to a real decrease in the frequency of fruit consumption by carnivores due to

a seasonal shortage in the availability of ripe fruits (C. M. Herrera 1984a, 1985, Obeso 1986).

The total number of plant species represented in carnivore feces per 3-month period varied seasonally and with habitat disturbance level (Tab. 1). The seasonal pattern was similar in all habitats, with number of species increasing from June–August to a maximum in September–November, and then decreasing until March–May. The diversity of seed species was consistently higher in undisturbed than in lightly disturbed areas. For all seasons combined, feces from undisturbed areas contained seeds from 19–23 species, while those from disturbed ones yielded seeds from 12–18 species. Several species either disappear or have much reduced importance in the feces collected in disturbed areas. Prominent among these are *Arbutus unedo*, *Crataegus laciniata*, *Juniperus phoenicea*, *Sorbus domestica* and *S. torminalis* (Tab. 1).

Seed-containing feces most often had no or few remains of animal prey. On average, an estimated $19 \pm 29\%$ (median = 5%; N = 1535) of fecal volume was made up of remains of animal prey (insect exoskeletons, bones, feathers, hairs). Thirty-seven percent of all feces examined had no detectable animal remains, the entire content being made up of seeds and fruit skins. A further 37% had an estimated 5–20% in volume made up of remains of animal prey.

Tab. 3. Summary of analyses performed on fruit characteristics and pulp chemical constituents to compare species sets eaten (N = 23) and not eaten (N = 33) by carnivorous mammals in the study region. Separate analyses were conducted on fruit characteristics and pulp constituents.

Variables	Analysis of variance				Discriminant analysis			
	Univariate		Multivariate		Correlation with canonical variable	% Correct classifications	Mean coordinates on CV	
	F	P	F	P			Eaten by mammals	Not eaten
Fruit characteristics:			13.8	<0.0001		81.8	1.263	-0.842
Fresh mass ^a	26.9	<0.0001			0.677			
Seed number ^a	4.8	0.03			0.287			
Individual seed mass ^a	0.1	0.93			-0.011			
Pulp/fruit mass ratio ^b	23.6	<0.0001			0.635			
Pulp constituents:			4.2	0.002		71.4	-0.876	0.657
Lipids ^a	0.03	0.87			0.031			
Protein	8.15	0.006			0.537			
Fiber	9.91	0.003			-0.593			
Soluble carbohydrates	2.03	0.16			0.268			
Total minerals	9.27	0.004			0.573			
Water content	2.05	0.16			0.269			

a. Variable log-transformed for the analyses.

b. Variable transformed with arcsin for the analyses.

Seed dispersal and predation

For all plant species, seasons and areas combined, only 0.89% of all the seeds found in feces (N = 148,167; excluding *Ficus carica* and *Arbutus unedo*, see below) were broken or cracked (Tab. 2). The remaining seeds were apparently intact. The proportion of damaged seeds varied among species. Almost all seeds of *Pistacia terebinthus* (98.5%) and an important proportion of *Juniperus communis* (37.5%) and *J. sabina* (14.3%) seeds found in feces were broken. All remaining species had < 10%, and most < 5% damaged seeds (Tab. 2). For *Crataegus laciniata*, *Taxus baccata*, *Viscum album* and *Vitis vinifera*, no broken or cracked seed was ever found in a combined total of 2682 seeds. For most species, therefore, fruit consumption by carnivores apparently resulted in seed dispersal. *Viscum album* is a conspicuous exception. Despite the fact that carnivores did not damage any seed of this mistletoe, all seeds found would have failed at survival because of the inappropriateness of the ground as a germination substrate for the species. The percentage of damaged seeds was not correlated with seed size across species (mass of individual seeds; $r_s = -0.060$; N = 19 species, P = 0.80).

I could not reliably determine the incidence of seed damage for *F. carica* and *A. unedo*, and these two species have been excluded from the computation of overall percent damage (Tab. 2). In the first case, some seed breakage did occur, but coat fragments of broken seeds were too small to allow reliable estimates of seed number. In the case of *A. unedo*, which has a thin and soft seed coat, no evidence was found of seed breakage, but the possibility exists that I missed seed coat remains from broken seeds.

Individual feces contained seeds from 1–5 different plant species, but most (66.9%) contained seeds of only a single species. Proportions of feces with 2, 3, 4 and 5 seed species were, respectively, 25.8%, 5.9%, 1.3% and 0.1%. Mean number of species per fecal sample was 1.4 ± 0.7 (median = 1 species/sample; N = 1535; all areas and seasons combined).

For all species, areas and seasons combined, individual feces contained an average of 140 ± 261 seeds (median = 49 seeds; Tab. 2). Average number of conspecific seeds per fecal sample varied broadly between species (Tab. 2), from 4.0 (*Sorbus domestica*) to 354.5 (*F. carica*) seeds. The mean number of conspecific seeds per fecal sample was negatively correlated with individual seed mass ($r_s = -0.641$, N = 20, P < 0.01). This means that, after dispersal by carnivores, seeds of small-seeded species tend to occur in denser conspecific clumps than those of large-seeded ones.

Correlates of fruit consumption by carnivores

In this section I examine the null hypothesis that species whose fruits are eaten by carnivores do not differ with regard to fruit and plant characteristics from other regionally co-occurring species whose fruits are not eaten by carnivores. The 56 species of fleshy-fruited plants occurring in the study region were divided, based on the results of the present study, into two groups: species eaten and species not eaten by carnivores (see Appendix). Fruit and plant features were then compared for the two sets of species. *Olea europaea* was excluded from all analyses, as it does not occur naturally in the study area. Differences in quantitative traits were examined using analyses of variance and discriminant analysis, with consumption by carnivores being the categorizing

Tab. 4. Differential representation of plant growth form and fruit color, scent and persistence after ripening, in the sets of species whose fruits were eaten (N = 23) and not eaten (N = 33) by carnivorous mammals in the study region.

Consumption by carnivores	Proportion of species (%)				Heterogeneity ^a	
					Chi-square	P
A. Growth form						
	Herbs	Shrubs	Woody Vines	Trees		
Eaten	0	30.4	4.4	65.2	21.2	<0.0001
Not eaten	15.2	54.5	21.2	9.1		
B. Color of ripe fruit						
	Black	Red + Orange	Brown	Other ^b		
Eaten	13.0	30.5	26.1	30.4	14.1	0.0018
Not eaten	45.5	36.3	0	18.2		
C. Scent of ripe fruit						
	Scentless		Scented			
Eaten	13.0		87.0		40.7	<0.0001
Not eaten	97.0		3.0			
D. Persistence after ripening						
	Persistent on plant		Falling to ground			
Eaten	26.1		73.9		35.0	<0.0001
Not eaten	100.0		0			

a. 'Exact Test' of Wells and King (1980) using the hypergeometric distribution.

b. Include white, blue and greenish fruits.

ing variable. Separate analyses were run for fruit structural and pulp chemical composition variables (Tab. 3).

A significant multivariate difference exists between species eaten and not eaten by carnivores with regard to fruit structural traits (Tab. 3). Univariate analyses reveal significant differences in fruit fresh mass, number of seeds per fruit, and the proportional importance of pulp mass with respect to total fruit mass. Species eaten by carnivores have fruits significantly heavier (2.23 ± 4.05 g), more pulp-rich ($68.9 \pm 18.6\%$ of fruit mass), and containing more seeds (60 ± 258 seeds), than fruits from species not eaten (0.25 ± 0.19 g; $47.1 \pm 14.3\%$; and 2.9 ± 5.9 seeds, respectively). The discriminant function classified correctly 81.8% of species into carnivore consumption categories on the basis of fruit structural traits examined here (Tab. 3).

There is also a significant multivariate difference between groups in the nutritional characteristics of fruit pulp (Tab. 3). Univariate analyses show significant between-group heterogeneity in protein, fiber and total mineral content. Lipid, water, and soluble carbohydrate content do not differ significantly between groups (Tab. 3). The fruit pulp of carnivore-eaten species have higher fiber content ($24.1 \pm 16.1\%$ pulp dry mass), and lower protein ($3.6 \pm 1.4\%$) and mineral ($3.1 \pm 1.4\%$) content, than species not recorded in carnivore feces (13.1

$\pm 8.1\%$, $4.8 \pm 1.5\%$, and $5.2 \pm 2.8\%$, for fiber, protein and minerals, respectively). The discriminant function correctly classified 71.4% of the species into carnivore consumption categories on the basis of pulp nutritional configuration (Tab. 3).

The proportional distribution of plant species among growth forms is different for the eaten and not-eaten groups (Tab. 4A). Trees are over-represented, and herbs and vines underrepresented, in the set of species eaten by carnivores. The proportions of species with different fruit colors are also significantly different in the eaten and not-eaten sets (Tab. 4B). Black fruits tended to be underrepresented, and brown and "others" (including white, blue and green) overrepresented, among species eaten by carnivores. Carnivores eat all species in the region having brown fruits, and only 16.7% of those with black fruits. Significant differences also exist between the two species groups in frequency of scented ripe fruits (Tab. 4C) and patterns of fruit persistence after ripening (Tab. 4D). Species eaten by carnivores tend to have scented fruits more often than species not eaten. Fruit species eaten are from plants that regularly abscise some fruits shortly after ripening. All regional species that abscise ripe fruits have been recorded in the fruit diet of mammalian carnivores.

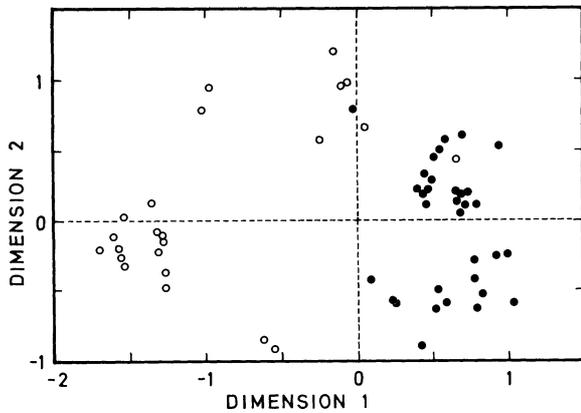


Fig. 1. Scatter diagram resulting from nonmetric multidimensional scaling analysis of qualitative traits of fruits occurring in the study region (see text for further details). Open dots, species found here to be eaten by carnivores; filled dots, species not eaten by carnivores.

As the qualitative traits examined here are correlated among themselves (Herrera 1987 and unpubl.), the possibility exists that separate analyses (Tab. 4) do not describe accurately the actual correlates of fruit consumption by carnivores. To elucidate this point, a similarity matrix between plant species was constructed considering simultaneously the four qualitative characters examined. Similarity scores ranged from 0 (no coincidence in any character) to 1 (coincidence in the four characters). All characters were weighted similarly, thus coincidence in any character added 0.25 to the overall similarity value. The matrix was subjected to nonmetric multidimensional scaling using procedure MDS in SYSTAT with the Guttman algorithm (Wilkinson 1986). Configuration was fitted to two dimensions, and scores of plant species on these axes were obtained. Species eaten and not eaten by mammalian carnivores have virtually nonoverlapping distributions on the plane defined by the two dimensions obtained from the analysis (Fig. 1).

Results show that the null hypothesis stated above must be rejected. Plant species eaten by carnivores differ from those not eaten with regard to plant growth form and fruit size, structure, pulp chemical composition, color, scent and persistence on the plant after ripening. This indicates that plant species eaten by carnivores represent a non-random subset of the regional fleshy-fruit producing flora with respect to the above features. Large, many-seeded, pulp-rich, brown, scented, tree fruits often falling to the ground after ripening, having a pulp high in fiber and low in protein and minerals, tend to be eaten by carnivores more often than fruits possessing other traits. Some of the species with the above profile (*Juniperus oxycedrus*, *J. phoenicea*, *Ficus carica*, *Sorbus domestica*, *S. torminalis*) are among those occurring most frequently in carnivores' feces (Tab. 1), though frequency will also be influenced by abundance in the habitat.

Discussion

The frugivory of carnivores

In the region studied, carnivores eat fruits throughout the year. The data available do not allow an estimation of the relative importance of fruits as a diet component, as only fruit-containing feces were examined. Previous investigations in central Europe and the Mediterranean area indicate, however, that fruits often are a major component of the diet of the three mammal species involved here. For *Meles meles*, fleshy fruits may represent seasonally up to 44–73% of total food biomass ingested (Kruuk and Kock 1981, Guitián Rivera and Callejo Rey 1983, Ciampalini and Lovari 1985, Lüps et al. 1987). For *Martes foina*, fruits account for 42–70% of total food biomass (Delibes 1978, Tester 1986), and for *Vulpes vulpes* reported figures range between 7–84% (Guitián Rivera and Callejo Rey 1983, Calviño et al. 1984a, Ciampalini and Lovari 1985, Goszczynski 1986). Similar levels of fruit consumption have also been reported for other carnivores like *Genetta genetta* and *Martes martes* in southern Europe (Delibes 1974, Garzón et al. 1980, Guitián Rivera and Callejo Rey 1983, Calviño et al. 1984b), further revealing that frugivory by carnivores is a widespread phenomenon. All these studies found that fruits contributed most biomass to the carnivores' diet in autumn–winter, but that frugivory occurred consistently for most or all of the year. The results of the present study, therefore, are not an exception in documenting extensive frugivory by European carnivorous mammals (see, e.g., Gipson 1974, Bullock 1975, Jaksic et al. 1980, Janzen 1986, and references therein, for reports of extensive frugivory among New World and African carnivores).

In the study region, the diversity (species richness) of species eaten by carnivores depended more on season and habitat disturbance level than on habitat type. On a yearly basis, carnivores ate a greater variety of species in undisturbed (19–23 species) than in disturbed (12–18 species) areas. Within each area, the highest diversity of fruits eaten occurred in the period September–November. No previous study in central or southern Europe has documented a taxonomic diversity in the fruit diet of carnivores comparable with that found in undisturbed forest in the present study. In other central and southern European studies the three species of carnivores considered here have been found to ingest fruits of 5–13 plant species (Goszczynski 1976, Delibes 1978, Amores 1980, Calviño et al. 1984a, Tester 1986). These figures fall in the range of those found here for lightly disturbed areas, and are much lower than those found for undisturbed forests. Most fruits reported as food of carnivores in the above studies were from cultivated plants, thus indicating that the animals foraged over severely disturbed, man-modified habitats. The possibility remains that the differences in the diversity of fruit species eaten by carnivores in my study region and elsewhere are partly due to differences in the inter-

annual component of diversity, as the present study combines data from many more years than most studies quoted above.

Fruit species disappearing (or decreasing in importance) from the carnivores' diet in slightly disturbed areas of the Sierra de Cazorla are mostly long-lived trees characteristic of later stages in the succession and having moderate to low population densities (*Arbutus unedo*, *Sorbus torminalis*, *S. domestica*, *Crataegus laciniata*, *Juniperus oxycedrus*, *J. phoenicea*; J. Herrera 1984, C. M. Herrera, unpubl.). These trees have been extirpated, or their densities much reduced, in disturbed areas, which explains why their seeds rarely if ever are found in carnivore feces in these areas. Even slight habitat alterations may thus produce a significant qualitative modification in the frugivorous diet of carnivores. As noted earlier, most studies on carnivores' diet performed in western Europe (including southern Spain) reveal a considerable importance of cultivated fruit species. The results of this study further suggest that the frugivory of carnivores in these man-modified habitats is but a depauperate reflection of the frugivorous habit they formerly had in natural habitats, and that only studies conducted in extensive undisturbed habitats may provide a realistic insight into the relationship between carnivores and wild plants, thus lending support to van der Pijl's (1982) contention quoted in the Introduction.

Seed dispersal

With the exception of *Pistacia terebinthus*, whose seeds are almost invariably destroyed, and *Viscum album*, whose seeds die after dispersal because of inappropriateness of the germination substrate, the carnivores considered here are legitimate dispersers of the seeds of the vast majority of fruits eaten. The proportion of seeds that become damaged after ingestion of fleshy fruits by mammals has been found in other studies to be directly related to seed size. Both cercopithecoid monkeys (Gautier-Hion 1984) and wild boars (*Sus scrofa*; Génard and Lescourret 1985) pass almost all the smallest seeds unharmed, while they destroy an important proportion of large seeds. In contrast, no relation between seed size and proportional damage was found here for carnivores.

Carnivores disperse the seeds of nearly 40% of the fleshy-fruited plants occurring in the region. The remaining 60% of species are entirely bird-dispersed (C. M. Herrera 1981, 1984a, and unpubl., Jordano and Herrera 1981, Obeso 1986). Most plants found here to be carnivore-dispersed also have their seeds dispersed by birds in the study region and elsewhere in southern Spain. These include well-known "bird-dispersed" plants such as *Prunus mahaleb* (Herrera and Jordano 1981), *Ficus carica*, *Rubus ulmifolius* (Jordano 1981, 1982), *Arbutus unedo*, *Sorbus torminalis*, *Crataegus*

monogyna, *Rosa canina* (C. M. Herrera 1984a,b), and *Juniperus* spp. (Obeso 1986). Seed dispersal by birds remains unrecorded to date for a few of the carnivore-dispersed plants (*Crataegus laciniata*, *Malus sylvestris*, *Prunus domestica*), but this may be influenced by their relative scarcity or insufficient study. In general, therefore, most or all carnivore-dispersed species have birds as well as mammals in their disperser coteries. No quantitative data are available at present to determine the proportions of seeds of these species that are dispersed by mammals and birds. These proportions most likely vary between species, and a broad gradient may be envisaged from predominantly mammal-dispersed (e.g., *Sorbus domestica*, *Arbutus unedo*, *Malus sylvestris*) to predominantly bird-dispersed (e.g., *Amelanchier ovalis*, *Crataegus monogyna*, *Taxus baccata*) (Herrera, unpubl.). A quantitative description of this gradient must await future investigations, but consideration of mammalian carnivores seems essential for a complete understanding of seed dispersal processes in the broad assemblage of Mediterranean species having mixed, bird-mammal dispersal.

In Mediterranean species with mixed seed dispersal, carnivores should produce seed shadows differing qualitatively from those produced by avian dispersers (Bullock 1975, Janzen 1986). This is most obvious with regard to the degree of clumping of conspecific seeds. For example, bird defecations may contain a maximum of 13 *P. mahaleb* seeds (Herrera and Jordano 1981), while up to 360 seeds of this species are found in single carnivore feces. Similar differences in the degree of postdispersal clumping between bird- and mammal-dispersed seeds exist for the other species with mixed dispersal (C. M. Herrera 1984b, Obeso 1986). For a species with mixed dispersal, one would expect seed and seedling mortality to differ between highly clumped, mammal-dispersed seeds, and scattered bird-dispersed ones (Wilson and Janzen 1972, Howe 1980, Bullock 1981, Augspurger and Kelly 1984, Janzen 1986). Similarly, spatial patterns of recruitment and average genetic similarity of neighbors may be hypothesized to differ for seedlings emerging from mammal- and bird-dispersed seeds of the same species. In areas without carnivores, therefore, plants with mixed dispersal may still be successfully dispersed by birds, but their seed shadows and demographic processes are probably different from those occurring in natural conditions, where carnivores disperse a certain proportion of seeds. This effect would be most pronounced for those species which, under natural conditions, have most of their seeds dispersed by carnivores, such as *Arbutus unedo*, *Sorbus domestica* and *Malus sylvestris* in my study region (Herrera, unpubl.). The long-term persistence of the populations of these plants probably depends on the conservation of carnivore populations. The true importance of carnivores as dispersers, however, will only be known with comparative work on the fate of seeds and seedlings from mammal dispersal vs bird dispersal.

Dispersal-related adaptations and the fruits eaten by carnivores

Fruits eaten by carnivores represent a nonrandom subset of the regional flora with regard to color, scent, persistence after ripening, size, structure and chemical composition of the pulp. Carnivore-dispersed plants tend to have large, many-seeded, pulp-rich, brown, scented fruits generally falling to the ground after ripening, with a pulp high in fiber and low in protein and minerals. Trees tend to be carnivore-dispersed more often than other growth forms. Interspecific variation in fruit traits has been often found to be associated with differences in the contemporary predominant dispersal agents in other studies as well (e.g., Janson 1983, Knight and Siegfried 1983, Gautier-Hion et al. 1985). Carnivorous mammals, however, have not been considered in any previous study of fruit characteristics, and features associated with consumption by these mammals are reported here for the first time.

Observed differences between species eaten and not eaten by carnivores in fruit size and color are difficult to interpret as adaptations (traits that promote fitness, regardless of whether they have evolved in connection with their current use; Gould and Vrba 1982) in relation to mammals alone. Species not eaten by carnivores are dispersed exclusively by birds, as noted above. The observation that carnivore-eaten fruits tend to be larger than those not eaten probably reflects bird-dispersed plants' adaptations as much as carnivore-related ones, since fruit size sets a limit to ingestion by the medium- to small-sized avian dispersers occurring in the area (Herrera 1985). A similar argument applies to fruit color differences, as black fruits, occurring predominantly among species not eaten by carnivores (i.e., exclusively bird-dispersed), are frequent among bird-dispersed plants (Wheelwright and Janson 1985). Observed differences in fruit seediness, relative pulp richness, and chemical composition of the pulp, between species eaten and not eaten by carnivores are difficult to interpret at present. Interspecific variation in several of these traits has some taxonomic correlates (Herrera 1987), and the differences found here may be partly related to the differential taxonomical composition of carnivore-eaten and not-eaten species groups (Appendix).

Two of the fruit features associated with carnivore consumption in southern Spain may be readily interpreted in terms of a proximate cause (fruit traits)-effect (carnivore consumption) relationship. Post-ripening abscission of fruits makes them accessible to ground-dwelling mammals, and scent would help them to locate fallen fruits (assuming that humans and carnivores have a similar perception of fruit smell). Furthermore, fruit scent and post-ripening abscission are closely associated across species. Most species (84.6%) with persistent fruits have scentless fruits, while most species (88.2%) with fruits falling to the ground have scented fruits ($P < 0.0001$, Fisher test). These two traits, and their corre-

lated variation across species, clearly appear as adaptations favoring endozoochorous seed dispersal by non-flying mammals.

Carnivore dispersal: the vanishing remnants of a pre-Holocene system

Differences in size, structure, color, scent, persistence, and pulp chemical composition between fruits eaten and not eaten by carnivores, determine the existence of two sets of species in the study region, each possessing particular sets of adaptations related to seed dispersal. Should fruit features associated with carnivore consumption be considered as plant adaptations related to seed dispersal by this particular mammalian group or, on the contrary, do these features correspond to a "generalized mammalian syndrome"? Several lines of evidence point to the second possibility.

The hedgehog (*Erinaceus europaeus*) was common in the Sierra de Cazorla in the recent past, but it has recently become a rare species there (Otero et al. 1978). I do not have data on the frugivory of this species in the area, but there are old reports from southern Spain demonstrating that it ate the fruits of some of the species found here to be eaten by carnivores (Darwin 1868). The brown bear (*Ursus arctos*) became extinct in the study area about 100 yr ago (J. A. Valverde, pers. comm.), but small relict populations still remain in northern Spain. Preliminary information on the diet of these populations (Garzón and Palacios 1979) demonstrate that this species eats the fruits of several of the plant eaten by southern Spanish carnivores (*Rosa* sp., *Prunus* spp.). The Barbary macaque (*Macaca sylvanus*), a cercopithecine monkey, was widespread over most of the Mediterranean Basin (including the Iberian Peninsula) from the Upper Pliocene to the middle or late Pleistocene (Zeuner 1959, Müller 1970, Delson 1980). Relict populations still persist in northern Africa, and some of them occupy habitat types very similar to those found in my study area (the nearest Moroccan populations are only about 400 km from the Sierra de Cazorla on a straight line). Extant populations of *M. sylvanus* in northern Africa have been reported to eat the fruits from at least 10 of the species eaten by carnivores in my study region (Fa 1986, Ménard and Vallet 1988, Mehlman 1988).

Further support to the notion that features of carnivore-eaten fruits should be interpreted in relation to a broad array of non-flying mammals, not just carnivores, comes from an examination of the use of wild fruits by local people still living in some areas of the Sierra de Cazorla (Herrera, unpubl.), as humans are also mammalian frugivores. Most (88.9%) of the wild fruit species ($N = 18$) eaten by local Cazorla people are also eaten by carnivores, while most (81.6%) of those fruits not considered edible by humans are also not eaten by carnivores ($P < 0.0001$, Fisher test). In this context, it is also revealing that an important proportion of the fruits

eaten by carnivores are the wild counterparts of, or are closely related to, cultivated fruit species (e.g., *Prunus*, *Ficus*, *Rubus*, *Vitis*). It is therefore not surprising to find that, in heavily man-modified habitats, carnivores readily shift to feed on the fruits of cultivated plants that are closely related to the plants whose fruits they eat in natural habitats (e.g., Skoog 1970, Amores 1980, Clément and Saint Girons 1982, Calviño et al. 1984a, Tester 1986).

The extant mammalian fauna of the Mediterranean Basin bears but a feeble resemblance to the mammalian fauna inhabiting the region before the large Pleistocene extinction (Zeuner 1959). During the Pleistocene, there were many more species of medium-sized, ground-dwelling mammals (including many carnivores related to extant ones) in southern European habitats than at present, and most of these became extinct by the end of that period (del Pan 1919, Zeuner 1959). On the other hand, the woody plants contemporarily dispersed by carnivores in western Mediterranean habitats represent a phylogenetically and biogeographically heterogeneous assortment of old taxa having varied origins in time (Cretaceous to Miocene) and space (paleotropical to northern temperate) (see Quézel et al. 1980). Most of these species were present in the Mediterranean Basin well before the mammalian extinctions took place (Quézel et al. 1980, Pons 1981). It may then be hypothesized that extinct mammals also ate their fruits, and that the situation in contemporary undisturbed Mediterranean habitats represents an impoverished version of the plant-mammalian interactions that took place when the diversity of mammals was higher than at present (analogously to the situation described by Janzen and Martin 1982 and Janzen 1984, 1985, 1986, for some New World habitats). The case of *Macaca sylvanus* noted above provides direct evidence in support of this hypothesis.

The likely impoverishment in plant-mammal interactions that the Pleistocene extinction brought about in the Mediterranean Basin would be analogous in its consequences to the further impoverishment that is taking place as a result of contemporary human-induced habitat changes and species eliminations. Nevertheless, even if contemporary quasi-undisturbed habitats would only provide a depauperate version of the original, pre-Holocene plant-mammal seed dispersal systems, we should still examine mammalian seed dispersal in these habitat remnants to understand the evolution of seed dispersal in species with mixed bird-mammal dispersal systems and, to use Janzen's (1976) words, "to serve as archivists for what were once powerful and complex interactions."

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Appendix. List of plant species with fleshy fruits occurring in the study region. Shown for each species are the two qualitative fruit traits used in the analyses that were not taken from Herrera (1987). Familial affiliation is shown only for species not eaten by carnivores (see Tab. 1 for eaten species). SC+ scented, SC– non-scented ripe fruits. P+ persistent, P– non-persistent (falling to the ground) ripe fruit.

Species not eaten by carnivores:

Arum italicum (Araceae), SC– P+; *Asparagus acutifolius* (Liliaceae), SC– P+; *Atropa baetica* (Solanaceae), SC– P+; *Berberis hispanica* (Berberidaceae), SC– P+; *Cotoneaster granatensis* (Rosaceae), SC– P+; *Cornus sanguinea* (Cornaceae), SC– P+; *Daphne gnidium* (Thymelaeaceae), SC– P+; *Daphne laureola* (Thymelaeaceae), SC– P+; *Daphne oleoides* (Thymelaeaceae) SC– P+; *Hedera helix* (Araliaceae), SC– P+; *Ilex aquifolium* (Aquifoliaceae), SC– P+; *Jasminum fruticans* (Oleaceae), SC– P+; *Ligustrum vulgare* (Oleaceae), SC– P+; *Lonicera arborea* (Caprifoliaceae), SC– P+; *Lonicera etrusca* (Caprifoliaceae), SC– P+; *Lonicera implexa* (Caprifoliaceae), SC– P+; *Lonicera periclymenum* (Caprifoliaceae), SC– P+; *Lonicera splendida* (Caprifoliaceae), SC– P+; *Paeonia broteroi* (Paeoniaceae), SC– P+; *Phillyrea angustifolia* (Oleaceae), SC– P+; *Phillyrea latifolia* (Oleaceae), SC– P+; *Pistacia lentiscus* (Anacardiaceae), SC+ P+; *Polygonatum odoratum* (Liliaceae), SC– P+; *Prunus prostrata* (Rosaceae), SC– P+; *Rhamnus alaternus* (Rhamnaceae), SC– P+; *Rhamnus myrtifolius* (Rhamnaceae), SC– P+; *Ribes alpinum* (Grossulariaceae), SC– P+; *Ruscus aculeatus* (Liliaceae), SC– P+; *Rubia peregrina* (Rubiaceae), SC– P+; *Smilax aspera* (Liliaceae), SC– P+; *Tamus communis* (Dioscoreaceae), SC– P+; *Viburnum lantana* (Caprifoliaceae), SC– P+; *Viburnum tinus* (Caprifoliaceae), SC– P+.

Species eaten by carnivores:

Amelanchier ovalis, SC+ P–; *Arbutus unedo*, SC+ P–; *Crataegus laciniata*, SC+ P–; *Crataegus monogyna*, SC+ P–; *Ficus carica*, SC+ P–; *Juniperus communis*, SC+ P–; *Juniperus oxycedrus*, SC+ P–; *Juniperus phoenicea*, SC+ P–; *Juniperus sabina*, SC+ P+; *Malus sylvestris*, SC+ P–; *Pistacia terebinthus*, SC+ P–; *Prunus avium*, SC+ P–; *Prunus mahaleb*, SC– P–; *Prunus domestica*, SC+ P–; *Pyrus* sp., SC+ P–; *Rosa*

canina, SC+ P+; *Rubus ulmifolius*, SC+ P+; *Sorbus aria*, SC+ P-; *Sorbus domestica*, SC+ P-; *Sorbus torminalis*, SC+ P-; *Taxus baccata*, SC- P-; *Viscum album*, SC- P+; *Vitis vinifera*, SC+ P+.

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