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Influence of type of avian frugivory on the fitness of *Pistacia terebinthus* L.

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Summary

The fruits of *Pistacia terebinthus*, a circum-Mediterranean tree/shrub, are consumed by an array of bird species that differ in feeding methods and in relative frequencies of visits to plants. In this study I document interindividual variation in the proportion of fruits consumed by three types of frugivores: legitimate dispersers, pulp-consumers and seed predators. The results show that the relative frequencies of each kind of frugivore notably influence the final reproductive output (absolute number of viable seeds dispersed) and in fact prevail over the effects of pre-dispersal factors acting on plant fitness. Those relative frequencies are not associated with any of the plant traits related to fitness, such as fruit crop size and the number of viable seeds produced, suggesting that the type of avian frugivory exerts a negligible, if not null, selective pressure on such plant attributes. Plant specialization to attract the most effective seed dispersers seems to be precluded, given the small scale at which the high variation in seed dispersal success takes place.

Key words: seed dispersal; avian frugivory; plant–animal interactions; Anacardiaceae; southeastern Spain

Introduction

The interaction that fruit-eating animals have with plants is important for plant demography and evolution for three main reasons.

(1) It has the potential to override the previous effects of pollination and fruit developmental phases on reproductive success, since it occurs at the final stage of plant reproduction (Herrera, 1988a; Jordano, 1989).
(2) Frugivores have certain foraging behaviours and fruit preferences directly related to plant traits (fruit size, number of seeds per fruit, etc.) with effects on fitness (e.g. Herrera, 1981; Levey, 1987, 1988; Snow and Snow, 1988; Howe, 1989; Jordano, 1989; Sargent, 1990).
(3) Frugivores determine to a certain degree the seed 'shadow' or patterns of seed deposition (Murray, 1988; Schupp *et al.*, 1989). These patterns, in turn, influence seed and seedling survival (e.g. Howe *et al.*, 1985; Schupp, 1988; Howe, 1989; Traveset, 1991).

Frugivores have been shown to differ in their contribution to plant fitness (effectiveness, *sensu* Schupp, 1993) (e.g. Snow, 1971; McKey, 1975; Murray, 1988; Snow and Snow, 1988; Jordano, 1989; Reid, 1989). Such effectiveness depends on both the quantity of seeds dispersed and the quality of seed dispersal. The quantitative aspect of frugivory is related to the number of frugivore visits and the number of seeds consumed per visit and it is important in determining effectiveness in some systems (e.g. Reid, 1989). On the other hand, the quality of frugivory is a function of (1) the seed treatment in the mouth and inside the digestive tract and (2) the ranging

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behaviour of the frugivores, which determines the probability that a deposited seed will survive and become an adult. See Jordano (1992) and Schupp (1993) for recent comprehensive reviews.

In the particular case of avian frugivory in the temperate zone, three major kinds of frugivores can be distinguished according to their feeding methods.

(1) Legitimate dispersers are those birds that swallow entire fruits, defecating or regurgitating the seeds.

(2) Pulp eaters, those that peck the fruit pulp and discard the seed, usually under the parent plant.

(3) Seed predators, which discard the pulp and break open the seeds to consume their contents.

There are no clear-cut limits in such classifications, so, in some circumstances a pulp eater can move a seed to a place suitable for germination and growth, a legitimate disperser may defecate seeds under the parent plant or under a conspecific with fatal consequences for the seeds or seedlings and a seed predator can act as a seed disperser by swallowing entire fruits (Snow and Snow, 1988; Jordano, 1992; personal observation). Moreover, a single bird species may be in a different category depending upon the plant with which it interacts (e.g. Howe and Vande Kerckhove, 1979; Levey, 1987; Snow and Snow, 1988).

The composition of the frugivore assemblage that visits a given plant population can vary spatially and/or temporally (Bronstein and Hoffmann, 1987; Herrera, 1988b; Snow and Snow, 1988; Fuentes, 1990; Guitián *et al.*, 1992; Jordano, 1993). This spatio-temporal variation has also been found for other mutualisms such as pollination (e.g. Herrera, 1988c; Horvitz and Schemske, 1990; Eckhart, 1992) or plant–ant systems (e.g. Barton, 1986; Horvitz and Schemske, 1990). We need to evaluate the extent of such variation and determine how it translates into variation in the selective pressures on the plant if we are to understand the evolution of any of these mutualistic interactions.

In the present study, I quantify the spatial variation at the individual plant scale in interactions between *Pistacia terebinthus* L. (Anacardiaceae) and the different birds that consume its fruits and consider the implications that these interactions have on plant fitness (estimated as a function of seed dispersal success) examining whether they can override ('screen-off', *sensu* Jordano, 1989) the effects of the events that took place during the pre-dispersal reproductive phases. I further examine how different plant attributes related to the plant–bird interaction may affect plant fitness.

The seed dispersal success to which I refer here depends only on the fruit-handling method, regardless of the final fate of the dispersed seeds and their probability of becoming adults. I consider that fruits removed either by pulp or seed eaters have a null seed dispersal success, even though, as mentioned above, a small proportion of the seeds might get to a 'good' place to germinate and become adults. Although not examined here, the effectiveness of the legitimate dispersers probably varies significantly among species. Differences in bird morphology, physiology and post-feeding behaviour make species different in their quality as dispersers (Hoppes, 1987; Malmborg and Willson, 1988; Schupp, 1993).

Study site and organisms

The study was performed during the fall and early winter of 1990 in Parque Natural de Cazorla, Segura y Las Villas, Jaén Province, in the southeast of the Iberian Peninsula. Observations were made at Las Navillas, located approximately 5 km from Vadillo-Castril, at an altitude of approximately 1000 m. The terrain is calcareous and very rocky and the vegetation consists of a secondary scrub dominated by *P. terebinthus, Quercus rotundifolia* and *Pinus pinaster.*

Pistacia terebinthus is a dioecious woody shrub or small tree, occasionally reaching a maximum height of 10 m. It is distributed all around the Mediterranean (Zohary, 1952). It produces small wind-pollinated flowers from mid-April through to the beginning of June. The fruits attain their final size approximately 1 month after flower anthesis and ripen during September; these fruits are drupes, 6.6 ± 0.7 (SD) mm long and 5.9 ± 0.7 mm wide on average ($n = 575$). Immature fruits are red and become green or bluish-green upon ripening. The drupes that fail to mature remain red and are either parthenocarpic (common phenomenon in the genus; Grundwag, 1976) or contain an aborted or insect-damaged seed (Traveset, 1993). As found in *Pistacia lentiscus* (Jordano, 1989), fruit ripening is strongly associated with seed viability.

Fruits in the study area are consumed by 20 species of birds, some of which are migratory (Traveset, 1993). Most species show a strong preference for the mature fruits; < 5% of the fruits removed are red. Most birds consume one to several fruits on a feeding visit. Pulp eaters handle a greater number of fruits per feeding bout than swallowers, although they also spend more time handling the fruits, thus decreasing the difference in the potential number of fruits consumed per unit time. Visit lengths tend to be longer for pulp eaters than for the other birds; aggressive displacement – which is one of the factors that may limit the length of a visit – has occasionally been observed in *Sylvia atricapilla* chasing off other species, such as *Sitta europaea* and *Parus ater*, from the tree (A. Traveset, personal observation).

Methods

A total of 18 plants were haphazardly selected for observations on fruit removal by birds in the fall of 1990. Each plant was observed daily for 30 min from 16 October to 4 November. Watches started at 8:30 am and continued until 6:30 pm. The time at which a plant was observed was randomly determined each day. Previous observations had been made on some of these plants between 21 September and 16 October (their feeding records are also included in the data presented here). The total time spent watching the plants, including the preliminary observations, was 163.25 h.

For each bird visit to a plant, the species, whether it fed on fruits, the colour of the fruits removed and the total number of fruits removed were recorded. In the present work, only feeding visits are considered.

For each observed plant, a number of variables that may be associated with the proportion of the mature crop consumed by the different frugivores were quantified: plant height, horizontal area of the canopy projection, total fruit production, initial number of mature fruits, number of fruiting conspecifics within a 10 m radius, peak ripening date (date at which the maximum proportion of the standing crop was mature) and degree of isolation from cover. The latter was measured as the mean distance between the plant and any other shrub or tree, conspecific or not, located in four 10 m long × 2 m wide transects; the first transect ran from the focal tree to the nearest tree or shrub and the remainder were set at 90°. A transect in which no plant cover was found received a measure of zero.

A correlation analysis tested for an association between any of the plant variables measured and the proportion of the crop taken by each of the three types of frugivores. I also performed a multiple regression analysis to examine the effect of a set of those plant variables on the absolute number of viable seeds dispersed (obtained as the product of the number of fruits that ripen and the proportion consumed by legitimate dispersers; this is a good estimate given that a ripe fruit has a probability > 99% of containing a viable seed inside). Angular transformations were used to increase the normality of the proportions. The variables included in the model of the regression had been logarithmically transformed previously. Straight means accompanied by standard deviations are given.

Table 1. Traits of each of the plants examined that describe size, fruiting phenology and isolation (in m) from any nearby woody vegetation and total bird visits and ripe (viable) fruits consumed during the periods of observations (in min) in each individual plant

Plant	Total fruit crop	Mature fruit crop	Peak ripening date	Days with mature fruits	Degree of isolation	Total bird visits	Total ripe fruit consumption	Total time of observations
77	12 000	6000	18	51	2.50	268	230	1320
92	3100	1395	20	55	8.50	25	24	690
100	6700	5025	27	58	30.80	87	81	450
103	5000	2250	20	48	6.38	51	35	450
104	17 500	11 375	14	56	8.50	69	48	690
121	800	400	24	46	7.50	15	3	390
127	1600	720	26	44	5.30	42	30	450
157	20 000	7000	20	57	6.63	46	14	420
160	10 000	3500	20	50	7.25	22	7	390
169	13 000	9750	17	60	5.00	261	241	450
171	11 000	6050	17	58	5.05	178	132	915
172	8000	2400	20	58	0.85	52	15	450
173	2000	400	24	55	2.28	47	18	390

Five of the 18 plants studied received few (<15) feeding visits during the observation periods and so were discarded from the data analyses. They did not differ from the rest in any measured trait. For all other plants, I consider that the proportion of fruits removed by a particular type of frugivore during the observations is a good estimate of the proportion of the crop removed by that particular type of frugivore.

Results

The mean number of feeding visits in the 13 plants considered was 89.5 ± 87.9, ranging from 15 to 268 (Table 1). Fruit removal increased rapidly to a peak in the last week of September and continued until the plants were depleted of ripe fruits. Most (>75%) of the ripe fruits were consumed between mid-September and late October. This pattern held for all 13 plants, regardless of the absolute number of fruits matured.

A total of 20 bird species (Table 2) was observed feeding on the fruits of *P. terebinthus*. Half were legitimate dispersers of the plant, five were pulp eaters and five were seed predators. The legitimate dispersers that consumed the most fruits were *S. atricapilla*, *Phoenicurus ochruros* and *Erithacus rubecula*. All pulp eaters were in the genera *Parus* and *Aegithalos*, while the main seed predators were *Fringilla coelebs* and *Carduelis chloris*. Considering all plants together, legitimate dispersers accounted for 46.9% of the ripe fruit removal, whereas pulp eaters and seed predators accounted for 34.2% and 18.9%, respectively.

There was extensive between-plant variation in the fraction of the fruits removed by the different types of frugivores (Fig. 1). Of the total number of mature fruits consumed, the proportion taken by legitimate dispersers averaged 28.3 ± 29.6% (range = 0–85.7%); this proportion was negatively correlated with that removed by pulp eaters ($r_s = -0.81$, $p < 0.001$, $n = 13$) but it was not associated with the proportion taken by seed predators ($r_s = -0.12$, $p = 0.70$), probably because of the low removal by these birds. The regression analysis in which the dependent variable was the absolute number of seeds dispersed included the following variables: total fruit production, total number of mature fruits, plant height and area and degree

Table 2. Consumption of *Pistacia terebinthus* fruits by birds

Species	TF	77	92	100	103	104	121	127	157	160	169	171	172	173	TFC
		Plant numbers													
Parus ater	P	X	X	X	X	X	X	X	X	X	X	X	X	X	
Parus major	P	X	X	X	X	X	X	X	X	X	X	X	X	X	
Parus caeruleus	P	X	X	X	X	X	X	X	X	X	X	X	X	X	416
Parus cristatus	P		X	X	X	X	X				X	X			(46.9%)
Aegithalos caudatus	P	X		X	X	X		X	X		X	X			
Sylvia atricapilla	D	X		X					X	X	X		X	X	
Sylvia melanocephala	D	X						X	X						
Sylvia communis	D	X													
Phoenicurus phoenicurus	D	X										X			
Phoenicurus ochruros	D	X		X					X	X	X		X	X	304
Erithacus rubecula	D	X		X	X	X		X	X	X	X	X	X	X	(34.2%)
Turdus philomelos	D										X				
Turdus merula	D	X													
Ficedula hypoleuca	D											X			
Corvus corone	D										X				
Sitta europaea	S	X		X						X	X	X	X	X	
Fringilla coelebs	S	X		X	X		X	X	X	X	X	X	X	X	
Dendrocopos major	S										X	X			168
Carduelis chloris	S	X									X				(18.9%)
Coccothraustes coccothraustes	S										X	X			

For each bird species, the type of frugivory (TF) (P, pulp eater; D, legitimate disperser; S, seed predator) and the individual plant visited are indicated. The number of fruits consumed and the proportion (in parentheses) it represents of the total fruit consumption (TFC) are given for each type of frugivory.

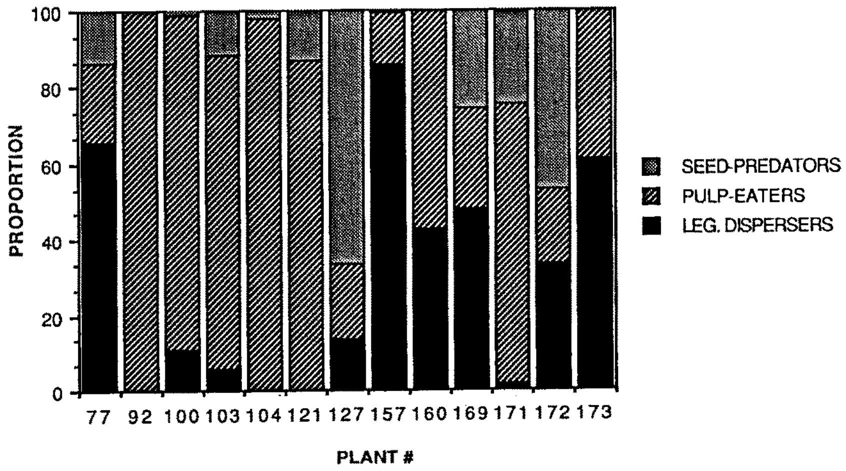

Figure 1. Proportion of the total number of mature fruits consumed by each type of frugivore, based on the 13 plants that received 15 or more bird visits.

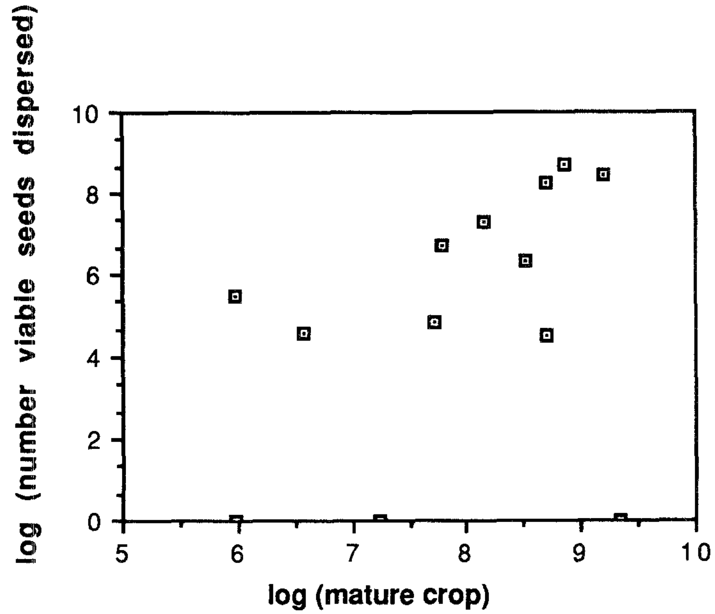

Figure 2. Relationship between the number of ripe fruits (viable seeds) per crop and the number of viable seeds consumed by legitimate dispersers from each crop; $r = 0.38$, $p = 0.20$.

of isolation. The model explained only approximately 5% of the variance ($F = 1.18$, $p > 0.05$) and none of the variables had any significant effect on the dependent variable. Interestingly, not even the absolute number of ripe fruits produced by the plant appears to influence the quantity that is consumed by legitimate dispersers (see Fig. 2); a plant that matures few fruits may have a greater number of seeds dispersed than another with a much greater mature fruit crop (see Table 1 and Fig. 1). Three of the plants (92, 104 and 121) had no fruits consumed by legitimate dispersers, however, nothing extraordinary was observed in them and they did not differ significantly from the other individuals in any of the variables measured. It appears, then, that the relative frequencies of each kind of frugivore visiting *P. terebinthus* can notably affect the absolute number of viable seeds dispersed, prevailing over the effects of pre-dispersal factors acting on plant fitness.

The total crop varied among plants (8515 ± 6112 fruits; Table 1) and was not correlated with the proportion of ripe fruits (viable seeds) produced ($r = 0.25$, $p = 0.40$). Plant height and basal area were not significantly related to total fruit crop sizes, to the proportion of mature fruits or to the number of mature fruits. There was a high synchrony in the maturation period among individual plants; all peak ripening dates occurred between 14 and 27 September. The number of days that plants bore mature fruits ranged from 44 to 60, with a mean of 54 ± 5 days. None of these variables was significantly related either with the type of frugivory or with the absolute number of seeds dispersed (all p-values $\geqslant 0.05$). The number of fruiting conspecifics within a 10 m radius varied from 0 to 8, with a mean of 4 ± 2 ($n = 13$) and was not related to any of these two variables either. The degree of isolation appeared to be significantly associated with the proportion of fruits removed by pulp eaters ($r = 0.60$, $p = 0.03$), indicating that the more isolated plants (with less available perches and nearby cover) had a higher probability of having their fruits removed by these birds.

Discussion

The interindividual variation in the relative frequency of visitation by each type of frugivore was great; some plants had most fruits consumed by legitimate dispersers whereas others were mostly visited by pulp or seed eaters and, thus, had a null or almost null dispersal success. The results showed that the frugivore assemblage visiting a plant can change dramatically the reproductive output produced by the effects of the other factors acting during the pre-dispersal phase. Plants that produce a large final mature crop do not necessarily have more seeds dispersed successfully than others that suffer greater losses during the previous reproductive stages and have small mature crops. The reproductive success of an individual of *P. terebinthus* is thus ultimately controlled to a large extent by the type of frugivores that eat its fruits and not only by the losses during the pre-dispersal phase. These results contrast with those obtained by Jordano (1989) in *P. lentiscus*. The cause of such differences is very likely the greater proportion of legitimate dispersers (19 species of a total of 26 frugivores; see Table 2 in Jordano (1989)) visiting that plant; in Jordano's (1989) study site (southwestern Spain), the non-legitimate dispersers had an irrelevant effect, reducing the seed dispersal success of an individual plant <4% on average. The situation with *P. terebinthus* in this study's site is quite distinct, with the legitimate dispersers actually consuming a lower percentage of fruits than the pulp and seed eaters (40.2 versus 59.8%, respectively).

The variation observed among individuals of *P. terebinthus* in the relative frequencies of visits by each kind of frugivore could not be explained by attributes inherent to the plant such as those that describe size (height, basal area), fecundity (total crop, absolute number of mature fruits) or phenology (days with mature fruits, ripening peak date). The effect of the measured plant traits on the number of seeds dispersed appeared to be negligible, suggesting that the potential for ongoing natural selection on those crop traits may be rather weak. This also contrasts with the findings of Jordano (1989), who reported that fruit crop size and the proportion of viable seeds explained a significant proportion of the variation in the number of seeds dispersed.

Studies examining the effect of crop size on seed removal rate have yielded different results depending upon the plant species; some have demonstrated an important effect of the crop size variable (e.g. Howe and De Steven, 1979; Denslow, 1987; Murray, 1987; Sargent, 1990; French *et al.*, 1992; Willson and Whelan, 1993), while others have not (Manasse and Howe, 1983; Davidar and Morton, 1986; Burger, 1987) or have shown it inconsistently among years (Foster, 1990).

Fruit dimensions were not measured in this study mainly because the coterie of birds visiting *P. terebinthus* appears to handle the whole range of fruit length and diameter (A. Traveset, personal observation). Jordano (1989) found that fruit traits (including nutrient composition of the pulp) in *P. lentiscus* had no relevant effect on seed dispersal success and it seems quite likely that the same occurs in *P. terebinthus*.

Manasse and Howe (1983) noted that individual trees differing in their relative position within a given habitat can differ markedly in the particular frugivore assemblage visiting the tree. In the present case, the most isolated plants were mostly visited and had most fruits consumed by pulp eaters. This is not surprising considering the microhabitat selection of the birds that have these handling methods; the pulp-eating Paridae are usually observed in open habitats and are not as elusive as legitimate dispersers such as *Turdus* spp. or *Sylvia* spp. (P. Jordano, personal communication, A. Traveset, personal observation).

The number of fruiting individuals in a 10 m radius failed to explain any variation in the proportion of fruits taken by different frugivores. Some studies have suggested that there is intraspecific competition for a limited frugivore assemblage, individuals in clumps having a lower fruit removal than isolated ones (e.g. Moore and Willson, 1982; Mannasse and Howe, 1983; Denslow, 1987). Other studies have shown the opposite (supporting the 'enhancement hypothesis', e.g. Sargent, 1990) and others have not found any influence of neighbours at all (e.g. French *et al.*, 1992). In the present case, no significant relationship was found between the number of days that viable fruits remained on the plants and the number of fruiting neighbours. All plants were depleted of viable fruits and frugivores did not appear to be limiting (although legitimate dispersers might have been).

With these results, it is difficult to imagine that frugivores in this system are exerting a strong selection on any measured plant trait directly related to fitness. The high variability in the frugivore assemblages visiting different individual plants and its lack of association with intrinsic plant traits, leads one to think that seed dispersal success probably has a largely stochastic component. Data from more fruiting seasons should show whether there is consistency in the avian species visiting the same individual plants. However, even if there is a strong consistency, it would probably be due to some external factor (such as position in the habitat), not genetically controlled by the plant and, thus, with no potential for being selected for or against.

At a larger scale, significant variation in the species composition of the avian consumers of the fruits of a plant species has been found when comparing different habitats or localities (e.g. Howe and Vande Kerckhove, 1979; Herrera and Jordano, 1981; Bronstein and Hoffmann, 1987; Herrera, 1988b; Fuentes, 1990; Guitián *et al.*, 1992; Jordano, 1993). The variation might also be temporal. In the southern Iberian Peninsula, fall abundances of *E. rubecula* and *S. atricapilla* fluctuated more than 4-fold over a 9 year period (Herrera, 1988d) and there is further evidence that a frugivore may be abundant one year and absent the next (Thompson and Willson, 1979; Snow and Snow, 1988). Also, even if present, a frugivore may not visit the plant at all because of changes among years in its fruit choice, as has been found by Malmborg and Willson (1988). Temporal differences in the composition of the frugivore assemblage visiting *P. terebinthus* might depend, for instance, on the availability of other fruits or food resources in the area, which may vary considerably among years.

Such spatio-temporal variation, occurring at all scales, in the relative composition of frugivorous species probably makes selective pressures acting on plant traits inconsistent and/or contradictory (Howe, 1984). In general, the fact that external factors (such as seasonality, between-year variation in fruit supply and number of other frugivores, habitat structure and abundance of alternative food resources) influence the ranging behaviour and foraging efforts of birds makes the fruit removal/seed dispersal phase a largely stochastic process. This stochasticity is what precludes or considerably decreases the possibility of any kind of plant specialization attracting the most effective dispersers.

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