

Pre-dispersal biology of *Pistacia lentiscus* (Anacardiaceae): cumulative effects on seed removal by birds

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This paper examines within-population variation in realized fecundity of *Pistacia lentiscus* (Anacardiaceae) and considers how plant traits relevant to the interaction with avian seed dispersers do influence it. A highly variable fraction of final-sized fruits (on average, 80.1% and 55.5% in two consecutive study years) contained empty seeds, either because of embryo abortion or parthenocarpy, but these fruits were retained and eventually consumed by birds. A total of 26 bird species consumed the fruits, with 19 of them being seed dispersers accounting for the removal of 82.5% and 83.3% of the final-sized fruit crop in two study years. Only four bird species removed 82.2% of the seeds and pulp/seed predators took 6.0%. Plant characteristics directly related to fecundity had strong effects on estimates of dispersal success relevant to fitness, accounting for 82.4% of its variance when holding constant the effects of fruit-design traits; the latter accounted for 1.8% of this variance. Fruit removal by frugivores had a negligible contribution to variation in realized reproductive output. This was largely attributable to the cumulative effects of the pre-dispersal phase, when great losses of potential fecundity occurred as abortion of embryos or production of parthenocarpic fruit. Variation in removal rates by frugivores did not “screen-off” these pre-dispersal effects.

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Introduction

Interactions with animal pollinators, seed dispersers and herbivores (including seed predators) are frequently a central element in the reproductive cycle of higher plants. Their different effects accumulate from the pollination throughout the seed-removal stage, having an ultimate influence on reproductive output in the form of dispersed seeds. A usual approach in the study of plant/animal interactions and their evolutionary consequences has been to consider only a single stage of the cycle (pollinators, herbivores, seed dispersers/predators, etc.) and examine the factors associated with inter-individual differences in some estimate of fitness (for a review, see Futuyma and Slatkin 1983). While this approach has been extremely useful in generating information about the natural history of the interactions involved and in identifying major effects on plant reproduction associated with each process, the demographic

consequences extracted are not necessarily relevant in an evolutionary context (Heithaus et al. 1982, Schmitt 1983, Herrera 1988).

Recently, several authors have critically examined this approach in the particular context of seed dispersal by vertebrates, and have identified major constraints in the evolution of dispersal-related plant traits (e.g., Wheelwright and Orians 1982, Herrera 1984c, 1985a, 1986, Howe 1984, Wheelwright 1989). A number of factors affect plant reproduction by determining losses of potential seeds from the flower-bud stage through the dispersed-seed stage (i.e., the pre-dispersal phase, Solbrig 1980). Since these stages are not independent (Primack 1987), considering them as isolated events may lead to erroneous conclusions about the evolutionary importance of a particular factor. Counterselection might occur between successively-acting factors and both the additive and multiplicative causal links between them must be considered. Further, variation in

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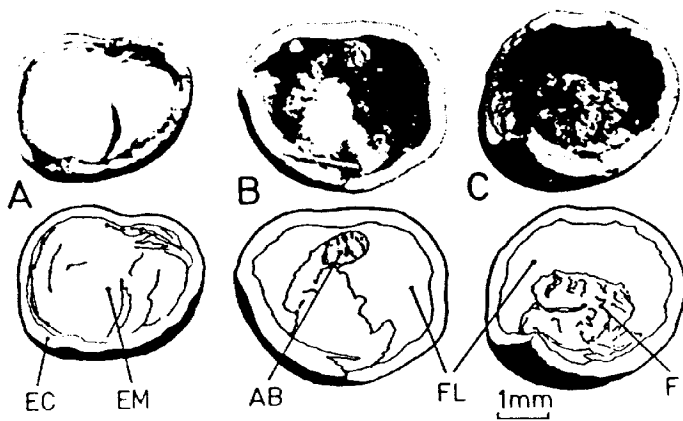


Fig. 1. Cross sections of *Pistacia lentiscus* seeds with exocarp and mesocarp removed. A: filled, viable seed showing normal development with all the inner space of the seed (locule) occupied by embryo and cotyledons (EM); EC: external seed coat. B: aborted seed showing considerably enlarged funiculus and ovule (AB) not filling up the fruit locule (FL). C: seed from parthenocarpic fruit, with a large locule (FL) and vestiges of funiculus and ovule (F). See also Grundwag and Fahn (1969) and Crane (1975) for similar information in other *Pistacia* species. Fruits collected at the study area, November 1982.

plant traits related to each factor must be linked directly to among-individual variation in seed output. Lastly, if necessary and sufficient conditions for natural selection to occur are met (Roff 1980, Endler 1986) both genetic and phylogenetic constraints can offset any selection differential, with the result that adaptive change (*sensu stricto*, see Gould and Vrba 1982) may not occur.

At least four important pre-dispersal factors can be identified as potentially limiting plant reproduction: ineffective pollination, fruit/seed abortion, pre-dispersal herbivory (including fruit/seed predation) and, in cases of animal dispersed seeds, failure to attract the appropriate dispersal agent. As stressed by Hainsworth et al. (1984), it is important to assess the net results of the interactions involved before assigning importance to any one. The higher-order effects resulting from intercorrelations between each factor are difficult to predict from the consideration of their summed contributions, with the result that the final effect on fitness cannot be predicted from consideration of each factor separately (e.g., Louda 1982, Heithaus et al. 1982, Herrera 1984a, b, 1988, Manzur and Courtney 1984, Heithaus 1986, Jordano 1987a).

For an interaction to be relevant to the selective regime experienced by a plant population, individual variation in seed output due directly to that interaction must be present. To the extent that 1) variation in seed output associated with the interaction under consideration actually results from the influence of a correlated factor and/or 2) variation in a trait relevant to the interaction is irrelevant to fitness, the interaction in question is not part of the selection pressure on the plant trait considered (Herrera 1988). Otherwise, the factor is a selective agent that has the potential to at least induce demographic changes in the population

(Heithaus et al. 1982). However, because of genetic and phylogenetic constraints, these demographic changes need not translate into adaptive change; for example, the trait in question may have low heritability value (Endler 1986). To study plant/animal interactions as selective agents in the evolution of the involved partners (coevolution), we must identify how these two levels, demographic and adaptive, are integrated.

This study was designed to provide information about factors limiting seed dispersal in *Pistacia lentiscus* L. (Anacardiaceae), a fleshy-fruited shrub with bird-dispersed seeds. Specifically, I document within-population variation in realized fecundity (i.e., dispersed seed), a main component of fitness, and examine how plant traits relevant to the interaction with frugivorous birds influence this component. Additionally, I assess the relative importance of several factors causing losses of reproductive potential from open flower through seed removal from the plant. Both "intrinsic" factors, such as rate of fruit abortion, and those resulting from the interaction with animals (seed predators, seed dispersers) result in loss of reproductive potential. I evaluate the relative importance and variability of each factor with regard to seed production by *P. lentiscus*.

Natural history of the plant

P. lentiscus is a dioecious woody shrub which dominates vegetation at the study site as well as other formation in the Guadalquivir lowlands (Herrera 1984c). Detailed observations on floral biology and pollination have been reported elsewhere (J. Herrera 1987, Jordano 1988). Flowering is between mid March and the end of April, just preceding vegetative growth. The species is wind-pollinated, with male flowers, grouped in inflorescences of 8–10 flowers, producing 47–60 10^3 pollen grains/flower and female flowers showing one seminal primorde.

The interval between the peak flowering date and the date with peak availability of ripe fruits ranges between 147 and 231 d for the studied plants (see below). After pollination, the fruits remain approximately 3 mm in diameter for 10–11 wk with no obvious growth. Final size is reached in 50 d after growth begins. In species of the genus *Pistacia*, this long period of fruit development is related to an extended dormancy of the zygote caused by a delay in singamy (Grundwag 1976). The final-sized fruit does not necessarily include a viable seed (Fig. 1). Fruits with viable seed show a characteristic green "content", filling all the seed locule (Fig. 1A). Empty seeds can result either from embryo abortion (Fig. 1B) or from unpollinated flowers yielding a parthenocarpic fruit (Fig. 1C). Grundwag and Fahn (1969), Grundwag (1975, 1976) and Crane (1975) discuss the causes of these types of seeds and describe in detail the associated degenerative morphology.

Final-sized fruits with empty seeds are not abscised but are retained on the plant and eventually become

desiccated if not consumed. Fruits are initially red, becoming glossy black after ripening 10–15 d after attaining final size. Ripening, and consequently acquisition of black colour, of a given fruit is selective and strongly associated with seed viability: only 5.8% of 1867 ripe fruits contained empty seed and only 6.6% out of 2603 unripe fruits (red colour) had viable seed ($\chi^2 = 3620.0$, $P \ll 0.0001$). Frugivorous birds consume both unripe and ripe fruits, but they show strong preference for black, ripe fruits during feeding trials (P. Jordano, pers. obs., Herrera 1984c, see below). The most important insects damaging the pulp and seeds in final-sized fruits of *Pistacia* spp. are chalcidoid hymenopterans that consume the seed content and gelechiid moths whose larvae eat the pulp (see Davatchi 1958 for a detailed account).

Study area and methods

Study site

I studied a population of *P. lentiscus* located at "Hato Ratón", a site 4 km SW from Villamanrique de la Condesa, Sevilla province, southwestern Spain, between January 1981 and March 1983. Vegetation is a tall sclerophyllous scrubland (2.5–5 m height) dominated by *P. lentiscus* (33.4% cover) and other fleshy-fruited shrubs and treelets such as *Olea europaea* var. *sylvestris* (Brot.), *Phillyrea angustifolia* L. and *Rhamnus lycioides* L. Descriptions of similar formations can be found in Rivas-Martínez et al. (1980). The study site is at 15 m elevation, in the lowlands of the Guadalquivir valley. The climate is of Mediterranean type, with dry, hot summers and cold wet winters. Annual temperature and rainfall average 18.1°C and 539 mm yr⁻¹, respectively.

Methods

Plants and fruits

A total of 20 individually marked female plants were studied, with intensive observations on fruiting phenology and fruit removal on 12 of these. An additional sample of 12 plants was added for data on fruit crop sizes and seed viability (see below). Weekly counts of fruits at marked branches were used to obtain estimates of standing crops of unripe, ripe, and damaged fruits as well as pre-dispersal loss of fruits. These periodic counts were made on 10 plants (N = 3114 fruits) in 1981–82 and 12 plants (N = 6394 fruits) in 1982–83.

During the 1982 flowering season, individual inflorescences were tagged on 6 plants, totalling 1493 flowers; abortion rates of flowers and undeveloped fruits were recorded for each inflorescence (see Jordano 1988 for details).

Crop sizes of final-sized fruits were estimated by complete count on all marked plants by early September, just before ripening. Fruits were sampled each year to record the frequency of viable seed among these final-

sized fruits. A total of 1500 fruits were collected from 29 plants in 1981, and 4470 fruits were sampled from 32 plants in 1982. Fruits were collected at final size, prior to ripening, from randomly chosen branches. Each seed was dissected to determine presence of embryo and cotyledons ("viable" seed hereafter), aborted embryo ("aborted" seed hereafter), and presence of insect damage to the seed content. Parthenocarpic fruits were identified by the absence of an enlarged embryo and presence of vestiges of the funiculus. The possibility exists that some abortions of non-enlarged embryos could be identified as parthenocarpic fruit, but the examination of aborted and parthenocarpic seeds resulting from experimental pollinations and pollen exclusions (Jordano 1988; also Crane 1975) revealed in most cases strikingly different morphologies (Fig. 1).

Several fruit variables were measured in samples (N = 30) of ripe fruits from the intensively-studied plants. These included fruit diameter, and fresh and dry weights of the pulp and seed (sum = whole fruit) (see Jordano 1987a for details). Chemical analyses of both the organic and mineral contents of the pulp of individual plants were carried out at "Centro de Edafología y Biología Aplicada", C.S.I.C., Salamanca, Spain, following procedures described in detail in C. M. Herrera (1987).

Birds

Mist nets were used to capture birds and obtain faecal samples for diet analyses. These were carried out according to the technique described in Moody (1970; see also Ralph et al. 1985). Faecal samples were analyzed individually, estimating visually the % volume made up by animal and vegetable matter. Seeds were identified and counted, the remaining vegetable material being examined with a microscope (100×) to identify additional fruit species in the sample from the presence of pericarp tissue remains. These remains were compared with a reference collection of microphotographs. For each fruit species in the sample, its percent contribution to the vegetable (fruit) volume was determined by estimating the amount of pericarp present and the minimum number of fruits yielding this amount of material. Further details can be found in Herrera (1984c) and Jordano (1987a, b).

Most of the vertebrate-damaged seed and fruit resulted from the action of greenfinches (*Carduelis chloris*, see below). Greenfinches take fruits of *P. lentiscus*, peel off the pulp and split the seed in half, consuming the seed content. I counted the remains of seed coats present in 25 quadrats (625 cm² each) regularly scattered on the ground beneath the canopy of the intensively studied plants. Seed coats were counted at the end of the fruiting season (late February) and the total loss of seeds due to the activity of greenfinches at each plant was estimated by dividing this figure by the proportion of the sampled area (projected canopy).

Fruit preferences were tested on caged individuals of

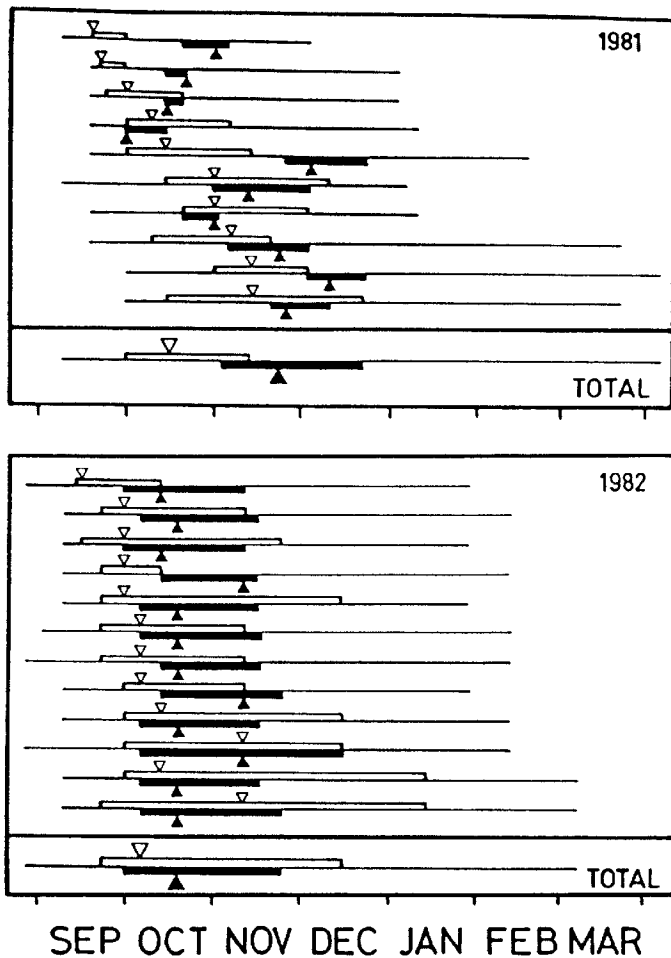


Fig. 2. Fruiting schedules of individual *Pistacia lentiscus* plants in the two study years. For each plant, the solid line encompasses the whole period of fruit availability; open bars and filled bars indicate the period when > 50% of the unripe and ripe fruits, respectively, are available. Arrows indicate the date with peak availability of both unripe and ripe fruits. The population fruiting schedule is illustrated by the inset labelled "TOTAL".

Sylvia atricapilla and *Erithacus rubecula*, two main seed dispersers of *P. lentiscus*. Two trials of preference tests were run for each species consisting in a mixed offer of ripe (black colour) and unripe (red colour) *P. lentiscus* fruits directly attached to the branch sampled from the plant. Trials lasted 4 h for each of 3 birds per species. Fruits of the two colours were offered roughly in the same proportions in each trial, including at least 50 fruits per trial. During the experiments I recorded the bird's choices and the order of consumption of fruits of different colours. Significance of the preferences was tested with the runs test, indicating if fruits differing in ripeness were consumed preferentially, i.e., in a particular order preceding consumption of the other fruits.

Data analysis

I used paired t-tests to compare the duration of ripe fruit availability, crop size, seed viability, and other fruiting traits for individual plants in different years.

The number of sampled plants differed between the two study years but only those individuals with repeated measures were compared.

A number of factors such as failure of pollination, fruit abortion, parthenocarpy, fruit/seed damage, etc., reduce the initial reproductive potential (in the form of 'potential seeds') by their action during the open-flower through the dispersed-seed stage. These reductions were quantified for each phase and regressed against the total loss of reproductive structures to determine the relative contribution of each stage to among-plant variation in total predispersal losses. This method is analogous to key-factor analysis (Podoler and Rogers 1975). The slopes of these regressions were used to assess the relative influence of each factor on variation in the magnitude of reduction of potential seed output between plants (see Heithaus et al. 1982 for a similar analysis and Maelzer 1970 for general applications to demographic studies).

I used multiple regression analysis to examine the relationships of the set of phenotypic variates of *P. lentiscus* plants (plant and crop sizes, seed viability, fruit traits, phenology) with the number of viable seeds consumed by avian dispersers, which may be taken as an estimate of the fecundity component of fitness, indicating realized seed output (see Lande and Arnold 1983). It must be explicitly stated here that the observational nature of this approach cannot distinguish characters directly determining fitness from those acting as correlated causes (Mitchell-Olds and Shaw 1987). Therefore, I use this analysis to evaluate hypotheses about the forces of selection, not to obtain quantifications of these forces. I pooled the available data on fruit removal and plant traits for the two study seasons to perform the analysis. Pooling the data was justified since a covariance analysis showed no significant between-year differences in the dependent variable when using each independent variable as the covariate. I obtained high variances associated with the Jackknife estimates of b and these can be attributed to multicollinearity, since it usually affects the computational stability of these parameters, yielding large sampling variances (Smith 1981, Mitchell-Olds and Shaw 1987). I decided to retain these estimates because a repeated analysis dropping plant size (correlated with final-sized fruit crop size) and seed dry mass and relative yield of pulp (correlated with fruit diameter) yielded similar estimates of b for the remaining variables. I tested for departures from normality in the original variables after standardization (zero mean, unit variance) with the Lilliefors test (Lilliefors 1967, in Wilkinson 1986), and variables showing significant departures from normality were transformed (see below and Tab. 5).

I divided the original independent variables in two sets, one grouping the "fecundity" traits (plant size, final-sized fruit crop size and % seeds viable), and another grouping the "fruit-design" traits (fruit diameter, relative yield of pulp and seed dry mass). A principal

Tab. 1. Statistics of fruit production per plant and proportion of seeds dispersed for *Pistacia lentiscus* in two study seasons.

Variable	Year	Mean \pm 1 s.e. [Range](n)
Number of flowers	1981	—
	1982	42 950 \pm 12 349 [1878–85 175] (6)
Number of fruits at final size	1981	10 567 \pm 1471 [660–29 200] (29)
	1982	12 181 \pm 1573 [1500–33 800] (31)
Proportion of fruits consumed	1981	0.825 \pm 0.040 [0.560–0.960] (10)
	1982	0.833 \pm 0.030 [0.671–0.953] (12)
Proportion of fruits with viable seed consumed	1981	0.232 \pm 0.054 [0.025–0.462] (9)
	1982	0.376 \pm 0.031 [0.194–0.605] (12)
Proportion of flowers contributing viable seed dispersed	1981	—
	1982	0.146 \pm 0.038 [0.059–0.323] (6)

component analysis identified these two groups as mutually independent sets: fecundity traits were associated with the first component, having factor loadings > 0.700 ; fruit-design traits showed low loadings (< 0.006) on this component and generated the second component, with loadings > 0.500 . Only these two components yielded eigenvalues > 1.0 and accounted together for 67.7% of the original variance. I tested the null hypothesis that the determinant of the population residual matrix after extraction of these two components was zero by means of an extension of the Bartlett's sphericity test (Cooley and Lohnes 1971, Cuadras 1981); the $\chi^2 = 7.43$ (d.f. = 5, $P = 0.191$) indicated that additional axes did not improve the analysis, justifying a separate treatment of each group of variables with these two components.

Results

Fruiting and ripening patterns

Full-sized fruits, either unripe (red colour) or ripe (black colour) were present on plants for a total of 205 d in the 1981–82 season and 191 d in the 1982–83 season, with extreme variation among individuals in the duration and timing of this phenophase (Fig. 2). Individual plants maintained a similar ordering in the fruiting sequence from one year to the next ($r_s = 0.867$, $P < 0.05$, $N = 12$), considering either the peak fruiting date or the initiation of the period when $> 50\%$ of the fruits are ripe (Fig. 2).

The duration of the fruiting period of individual plants (number of days with ripe fruits present) ranged between 76–196 d (1981–82) and 141–178 d (1982–83), with average values of 69 d and 149 d, respectively. The trend for a longer fruiting period in 1982–83 was general among individuals (paired $t = 2.94$, d.f. = 11, $P = 0.014$). There was a parallel trend towards earlier fruiting in 1982–83 (Fig. 2). For the whole population, peak

availability of ripe fruits occurred by 22 November (1981–82 season) and 19 October (1982–83), with a trend for individual plants to initiate fruiting 2 wk earlier, on average, in 1982 ($t = 2.10$, $0.05 < P < 0.10$) (Fig. 2). Thus, although individual plants maintained an ordered fruiting sequence in the two study years, they showed great variation in the timing and duration of the fruiting period between years.

Tab. 1 summarizes the available data on fruiting intensity of the studied plants. Female plants produced a highly variable number of flowers, ranging from 2000 to 85200 flowers. Extreme variation was also observed in fruiting intensity, measured as final-sized fruits (Tab. 1). Data on flower crop sizes were not available for 1981; however, the fruit crops (at final size) recorded in this year similar to those of 1982 ($t = 1.30$, d.f. = 27, $P = 0.268$, paired-sample test; Tab. 1).

Empty seeds in *P. lentiscus* result both from parthenocarp and embryo abortion (for a detailed account see Jordano 1988), with additional inviability due to insect seed predation (see below). A remarkable difference between the two years was observed in the proportion of fruits with viable seeds: $19.9 \pm 2.9\%$ ($N = 29$ plants, 1500 fruits examined) in 1981 and $44.5 \pm 2.2\%$ ($N = 32$ plants, 4470 fruits examined) in 1982, the difference being highly significant ($t = 6.74$, $P < 0.01$, d.f. = 27, paired-sample test). A result of this increase in proportional seed viability was a significant increase in the absolute number of viable seeds produced ($t = 4.85$, d.f. = 27, $P < 0.0001$, paired-sample test), yielding a great between-year variation in the quantity of viable seeds available for dispersal.

Fruit consumption and removal of viable seeds by frugivorous birds

The proportion of final-sized fruits consumed by birds (percent removal, hereafter) was very similar in the two study years, with $> 80\%$ of the fruit crop being consumed (paired-sample test with those plants with data

Tab. 2. Fruit consumption and relative importance of *Pistacia lentiscus* fruits in the diet of frugivorous birds at the study site. Information for 1981 and 1982 has been pooled. Disp., seed dispersers; Seed, seed predators; Pulp, eat pulp and discard seeds. Figures for fruit consumption include frequency of appearance of fruit remains in faecal samples (FAF), mean % volume made up by fruit remains (PV) and number of samples analyzed (n). PV for *P. lentiscus* indicates its % volume contribution to the whole fruit fraction of the diet. % removal indicates the fraction of seeds potentially dispersed or consumed by each species.

Bird species	Body mass (g)	Feeding type	Fruit diet			<i>Pistacia lentiscus</i>		
			FAF	PV	n	FAF	PV	% Seed removal
<i>Cyanopica cyanus</i>	72.5	Disp.	100.0	66.0	2	50.0	72.0	0.43
<i>Erithacus rubecula</i>	15.4	Disp.	91.0	68.0	289	85.8	65.3	11.29
<i>Ficedula hypoleuca</i>	13.6	Disp.	85.4	34.4	48	97.6	40.0	1.50
<i>Luscinia megarhynchos</i>	24.3	Disp.	19.6	3.7	46	12.0	30.2	0.18
<i>Muscicapa striata</i>	16.5	Disp.	66.7	14.7	15	100.0	20.0	0.39
<i>Phoenicurus ochruros</i>	19.0	Disp.	100.0	80.0	1	100.0	80.0	0.10
<i>P. phoenicurus</i>	15.8	Disp.	92.9	48.2	14	85.7	43.3	0.30
<i>Saxicola torquata</i>	14.8	Disp.	14.3	0.7	7	14.3	5.0	0.01
<i>Sturnus unicolor</i>	71.6	Disp.	100.0	80.0	3	100.0	62.0	2.20
<i>S. vulgaris</i>	76.2	Disp.						
<i>Sylvia atricapilla</i>	18.5	Disp.	98.7	86.1	634	93.6	65.3	48.79
<i>S. borin</i>	19.0	Disp.	100.0	92.4	153	84.9	50.4	11.89
<i>S. cantillans</i>	11.5	Disp.	90.5	68.3	21	66.7	60.3	0.75
<i>S. communis</i>	17.4	Disp.	90.9	70.9	11	54.6	82.0	0.61
<i>S. hortensis</i>	23.6	Disp.	100.0	66.0	5	100.0	44.4	0.29
<i>S. melanocephala</i>	11.5	Disp.	92.8	73.9	195	77.9	63.4	10.20
<i>S. undata</i>	9.1	Disp.	50.0	38.3	12	50.0	72.7	0.50
<i>Turdus merula</i>	86.9	Disp.	95.4	68.0	65	38.5	52.5	4.10
<i>T. philomelos</i>	67.0	Disp.	100.0	95.5	11	45.5	42.4	0.50
<i>Carduelis chloris</i>	23.6	Seed	68.8	59.5	76	67.1	81.0	1.90
<i>Columba palumbus</i>	459.5	Seed	100.0	81.9	11	90.9	80.9	3.90
<i>Fringilla coelebs</i>	21.5	Pulp	50.0	19.2	6	33.3	62.5	0.07
<i>Parus caeruleus</i>	9.5	Pulp	44.4	17.8	9	33.3	46.7	0.04
<i>P. major</i>	16.7	Pulp	14.3	11.4	7	14.3	80.0	0.04
<i>Phylloscopus collybita</i>	7.5	Pulp	8.4	0.1	83	0.04	1.8	0.01
<i>Regulus ignicapillus</i>	5.2	Pulp	12.5	0.01	8	12.5	1.0	0.01

available for the two study seasons, $t = 0.07$, NS, Tab. 1). However, the actual proportion of the final-sized fruit crop that contained viable seed and was consumed was only 0.232 (1981) and 0.376 (1982) (Tab. 1), largely due to a relatively large fraction of fruits with empty seeds (as described above). The between-year difference is highly significant ($t = 2.36$, $P < 0.001$, paired t-test). Estimates of fruit consumption by birds damaging the pulp or seeds (see below) were only available for 1982. These animals decreased the mean proportion of fruits with viable seed dispersed to 0.271 ± 0.025 (0.155–0.405) ($N = 12$ plants). When considering the initial size of the flower crop (data available for 1982 only, Tab. 1), the probability of an individual female flower yielding a dispersed seed is reduced to 0.146.

Individual plants showed a strong correlation between the absolute numbers of viable seed removed in the two years ($r_s = 0.762$, $P < 0.01$), indicating that they maintained their rankings in absolute fecundity from one year to the next in spite of extreme variation in seed viability. This was only attributable to stability in the fecundity differential among individual plants. Among-plant differences in seed viability or percent removal by frugivores did not offset the effects of this differential.

The low average percent removal of viable seeds in the two study years was not attributable to a lack of

reliance of the frugivorous birds on *P. lentiscus* fruits. A total of 26 bird species were recorded as fruit consumers in the study area (Tab. 2), 19 of them (73.1%) being seed dispersers. Three *Sylvia* species and the robin (*Erithacus rubecula*) accounted for 82.2% of the fruits consumed, pulp/seed predators taking only 6.0% of the fruits. *P. lentiscus* was the main fruit food for these frugivorous birds, representing $> 60\%$ of the fruit diet for, at least, 14 species of its disperser assemblage (Tab. 2). Strong reliance on *P. lentiscus* fruits for food in these birds typically encompasses the period September–February.

Observations of caged *S. atricapilla* and *E. rubecula* offered a mixture of red (unripe) and black (ripe) fruits indicated a strong preference for ripe fruits. In 2 out of 6 trials, birds started consumption of red fruits only after consumption of all the black fruits. For all 6 trials, birds showed a strong preference for the ripe, black, fruits whose consumption significantly preceded that of red fruits in the individual feeding bouts (runs test, $P \ll 0.001$ for all the trials). Since fruit ripening is selective and strongly associated to the presence of a viable seed, frugivorous birds apparently maximize the removal of viable seeds, i.e., frugivore choice results in a high probability that ripe, black, fruits with a viable seed will be consumed by a legitimate disperser. In a random

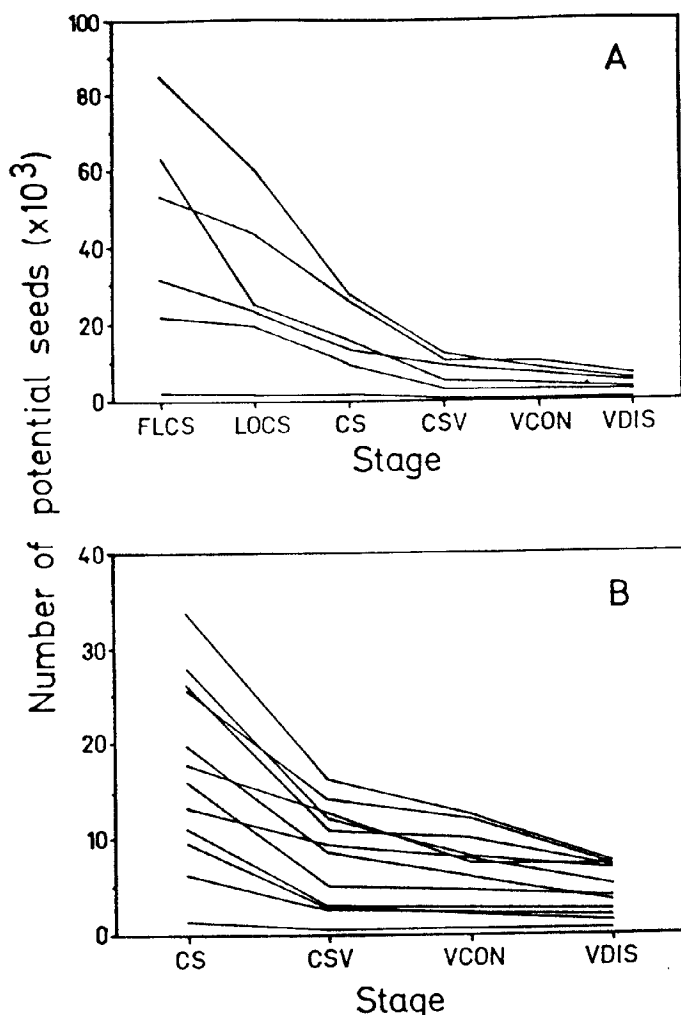


Fig. 3. Reduction of reproductive potential, expressed as maximum number of seeds, in successive phases of the reproductive cycle in female plants. Each line shows the patterns for an individual female *Pistacia lentiscus* plant, connecting the successive standing crops or realized seed output at different stages (abscissa). A: the whole cycle, from flower crop size (FLCS) throughout absolute number of viable seed dispersed (VDIS), with the intermediate stages of latent ovary crop size (LOCS, i.e., number of undeveloped fruits), final-sized fruit crop size (CS), absolute number of final-sized fruits consumed by frugivores (CSV), and absolute number of viable seed consumed by frugivores (VCON). B: patterns for the fruit removal-seed dispersal phase, including the data for the six plants shown in A plus an additional sample of six different plants.

sub-sample of the seeds recovered from the faecal samples of *S. atricapilla* in 1982 (N = 392) each seed was dissected to record the presence of a fully-developed embryo. Of these seeds, 92.1% were viable, 6.6% were empty, and 1.3% showed presence of an exit hole, indicating emergence of a seed predator (a chalcidoid wasp) after passage of the seed through the disperser digestive tract (see Chung and Waller 1986 for a similar report in *Rhus*). Thus, as indicated by the *S. atricapilla* sample, frugivorous birds remove a far greater fraction of viable seeds than expected from actual percent viability observed in the individual fruit crops. When considering the loss of ripe fruit to pulp/seed predators, the probability of removal for a viable seed by a legitimate disperser is 86.1%. Additional observations from other sites (Jordano and Herrera 1981, Herrera 1984c, Jordano, pers. obs.) suggest that this is a general interaction pattern in the lowland scrublands, where *P. lentiscus* fruits are one of the main food items of this abundant and diverse assemblage of frugivorous birds throughout the autumn and part of the winter. Neither a limited assemblage, both in diversity and abundance, nor a low reliance on *P. lentiscus* fruit for food appear as constraints on seed removal, since frugivorous birds consumed a high fraction of the available fruits.

Evaluation of factors influencing seed removal: cumulative reductions of crop size during the pre-dispersal phase

Since the factors resulting in failure of individual flowers to yield a viable dispersed seed act consecutively throughout the reproductive phase, their joint cumulative effect can be expressed as the proportion of initial crop size (female flowers) not reaching seed dispersal. The relative importance of the losses at each stage can then be quantified as the proportion of the initial crop size lost in that stage. The relevant information for the whole cycle is available for 6 plants in 1982 (Fig. 3A); data on seed losses during the fruit removal-seed dispersal phase are available for 12 plants (Fig. 3B). Tab. 3 summarizes the mean proportion of pre-dispersal losses of potential fecundity for the studied plants.

Approximately 55% of the initial crop is lost by abor-

Tab. 3. Main factors contributing to pre-dispersal losses in potential seed production in *Pistacia lentiscus*. Figures for the key-factor analysis indicate the slope of the regression of each factor on total loss of seeds and the corresponding correlation coefficient. Data (information for the two study years pooled) were log-transformed before analysis.

	Mean proportion loss	C.V.	Key factor	
			Slope	r
1. Flower abortion	0.2598	68.6	0.8119	0.9587 ***
2. Abortion of latent ovaries	0.2865	54.2	0.6866	0.9655 ***
3. Fruit not consumed	0.0473	68.3	0.5454	0.6641 **
4. Embryo aborted, parthenocarpic fruit	0.2211	49.4	1.1765	0.8570 ***
5. Seed damaged by insects	0.0041	143.5	-0.0183	0.0398 N.S.
6. Seed damaged by vertebrates	0.0365	96.1	0.4464	0.5741 *

*P < 0.05, **P < 0.025, ***P < 0.01, N.S. not significant.

Tab. 4. Variation in characteristics of individual *Pistacia lentiscus* plants, during the 1982 season, related to fruiting, ripening phenology, fruit design, and nutrient content of the pulp. This data set corresponds to the 1982–83 fruiting season (see text for further details).

Plant	Fruiting			Phenology			Fruit characteristics			
	Crop size	% viable seeds	Plant size ¹	Days in fruit	Rank in fruiting	Fruit diameter	Relative yield pulp ²	% Lipids	% Protein	% Ash
701	27800	44.0	16.6	155	10	5.5	0.400	–	–	–
702	33800	48.1	58.0	168	9	5.7	0.422	60.51	6.06	–
703	9500	30.8	13.9	168	12	5.4	0.417	57.19	6.50	0.25
704	17800	58.0	28.3	141	3	5.6	0.352	–	–	1.20
705	13400	69.8	47.8	155	6	5.2	0.434	–	–	–
706	26250	41.1	25.5	141	2	6.1	0.429	69.16	4.13	–
707	25800	55.3	33.2	178	5	5.2	0.404	60.29	4.75	0.38
709	1500	49.0	9.1	141	11	5.8	0.424	–	–	0.62
717	15900	32.4	20.4	178	8	4.8	0.425	59.31	4.44	–
720	19800	43.4	27.3	155	7	5.3	0.328	–	–	1.10
NMT2	6300	44.3	8.1	162	4	5.3	0.444	65.66	4.50	–
740	11000	27.0	15.5	154	1	5.2	0.386	–	–	0.05
Mean	17404	45.3	26.7	149	–	5.4	0.407	62.00	5.10	0.60
s.D.	9675	12.1	14.5	8	–	0.3	0.035	4.50	1.00	0.47

1. Area (m²) of the horizontal canopy projection.

2. Dry mass of pulp as proportion of the whole fresh mass of fruit.

tion of flowers or fruit-shedding in the initial stage of fruit growth (Tab. 3). After the period of about 3 months during which the tiny fruits remain at about 2 mm diameter, a sudden growth to final size occurs, but most fruits abort before this (Jordano 1988, see also Grundwag 1976). All the monitored plants consistently experienced the greatest losses in these two phases (Fig. 3).

As stated above, most final-sized fruits were consumed by frugivorous birds. However, when accounting for the fraction of those consumed seeds that actually were inviable, due to embryo abortion or parthenocarp, a great generalized reduction is observed in all plants (Tab. 3, Fig. 3). The estimated proportion of viable seeds reaching the adequate dispersal agent is further reduced by the probability of being damaged by insect seed predators or avian frugivores that damage pulp or seeds. Reductions attributable to seed predators are, on average, below 4% and show extreme between-plant variation in magnitude (CV > 90%), as compared with the "intrinsic" factors such as flower and fruit shedding and seed inviability (CV < 70%, Tab. 3, Fig. 3).

The "intrinsic" factors (flower abortion, abortion of latent ovaries and seed inviability) showed steeper slopes than factors associated to animal interactions (fruit/seed damage and lack of consumption by frugivores, Tab. 3). As indicated by the magnitude of the slope corresponding to each factor, the greatest contribution to between-plant variation in total loss of potential seed production is due to embryo abortion and production of parthenocarpic fruit, but note that this factor accounted for less ovule loss than flower or undeveloped fruit abortion (Tab. 3).

There are two additional patterns emerging from Fig. 3. The total variation of standing crop sizes among plants is greatly reduced throughout the continued effects of the above factors, with the range of initial flower crop sizes (1878–85175) reduced to a minimum of 606 and a maximum of 7622 viable seeds dispersed. The CV's decreased from 70.43% for the flower crop sizes to 58.32% for the number of viable seed dispersed. Note that the magnitude of the reduction in potential reproductive output was largely proportional to the initial potential reproductive output, plants with the largest flower crops experiencing the greatest absolute and proportional losses (Fig. 3). The rankings of the standing crop sizes after the action of each factor reducing reproductive potential were compared with the rankings at the previous phase (see Fig. 2). These fecundity rankings were significantly maintained at each transition (Kendall's coefficient of concordance = 0.998, P = 0.039, for the overall agreement among the rankings) but the fecundity differential was greatly reduced.

Correlates of seed removal: potential effects of avian frugivores

Plant traits can be examined to identify variables showing strong and consistent (between-individuals) associations to fitness variation. Tab. 4 summarizes the data available for the plants studied in detail during the 1982–83 season, including information on fecundity, phenology and fruit characteristics that might be relevant to variation in realized seed output.

The results of multiple regression analysis between plant traits (Tab. 4) and the number of viable seeds dispersed are summarized in Tab. 5, with the analysis

Tab. 5. Parameters of multiple regression relating number of viable seeds consumed by avian dispersers to characteristics of *Pistacia lentiscus* plants. Data (information for the two study years pooled) were log transformed before analysis (angular transformation was used with relative yield of pulp and proportion of viable seeds). For the whole set of variables, $R^2 = 0.958$, $F = 42.23$, $P < 0.0001$. Values of b and its standard error were estimated by means of a 'delete-one' Jackknife procedure.

Variable	$b \pm s.e.$	Standardized coefficient	t	r^2
Intercept	-0.489	-	-	-
Plant size	-0.216 ± 0.387	-0.071	0.56 N.S.	0.510
Crop size	1.003 ± 0.272	0.618	3.69 **	0.658
Proportion of seeds viable	2.010 ± 0.356	0.637	5.64 ***	0.646
Days in fruit	-0.272 ± 0.249	-0.053	1.09 N.S.	0.052
Fruit diameter	-2.654 ± 3.138	-0.076	0.85 N.S.	0.012
Seed dry mass	30.485 ± 56.229	0.007	0.54 N.S.	0.003
Relative yield of pulp	-1.114 ± 1.353	0.006	0.82 N.S.	0.024

N.S., not significant. ** $P < 0.002$; *** $P < 0.001$, d.f. = 20.

performed on the pooled data on fruit removal for the two study seasons and 12 plants, with 9 of them having repeated measures. The whole set of variables accounted for a significant fraction of variance in number of seeds dispersed ($R^2 = 0.958$, $F = 42.23$, $P = 0.0001$, Tab. 5). However, only the effects of fruit crop size and proportion of viable seed reached significance ($t > 3.69$, $P < 0.002$, d.f. = 20, Tab. 5), and both variables showed the highest values for the standardized coefficients, suggesting a strong effect on the dependent variable. Thus, plants with larger fruit crops and greater percentages of seed filling showed increased absolute number of viable seed dispersed.

To study the effect of avian frugivore activity on the number of seeds dispersed, I used percent removal (the fraction of full-sized fruits consumed) as the independent variable, while holding all other plant traits (Tab. 5) statistically constant. Percent removal failed to explain a significant fraction of variation in number of viable seed removed ($R^2 = 0.013$, $F = 0.252$, $P = 0.621$); therefore, increased frugivore activity did not outweigh the initial fecundity differential, having a negligible effect on variation in realized reproductive output.

Tab. 6 summarizes the results of testing hypotheses about effects of the 'fecundity' and 'fruit-design' traits (see Methods) on different fitness components. A post-hoc test showed that the simultaneous effect of the fecundity traits on the absolute number of viable seeds dispersed is highly significant ($F = 87.51$, $P < 0.0001$) while fruit-design variables have a negligible effect ($F = 0.506$, $P = 0.680$, Tab. 6). It must be noted that variables of pulp nutrient content (available only for 6 plants, Tab. 4) were not included in the regression model due to insufficient sample size but were also uncorrelated with the dependent variable ($r_s < 0.143$, $P > 0.375$ for all variables tested, Tab. 4). When relative fitness is calculated as a proportion of the initial fruit crop size (i.e., the usual approach of estimating the fraction of the fruit crop consumed, Davidar and Morton 1986), both sets of variables were insignificant in their effects (Tab. 6). Finally, fecundity traits showed a

highly significant effect on relative fitness, measured as the number of viable seed dispersed relative to the population average, but fruit-design traits had only marginal significance (Tab. 6).

In summary, plant characteristics directly related to fecundity, namely plant size, final-sized fruit crop and % seed viability, had highly significant effects on estimates of seed removal relevant to fitness, accounting for 82.4% of its variance when statistically controlling for the effects of the fruit-design traits; the latter accounted for only 1.8% of this variance when statistically holding constant the effects of fecundity traits. Variation in fruit removal by frugivorous birds did not outweigh these effects, having a negligible effect on variation in realized reproductive output (viable dispersed seeds).

Tab. 6. Summary of the effects of different groups of plant traits on various estimates of fitness components. For each group of variables, figures indicate the significance test of post-hoc hypothesis involving linear combinations of regression coefficients, i.e., hypothesis that the regression coefficient of the variables involved are simultaneously zero.

Fitness component	"Fecundity traits"*	"Fruit-design traits"*
Number of viable seed dispersed	$F = 87.51$ $P < 0.0001$ $R^2 = 0.952$	$F = 0.506$ $P = 0.680$ $R^2 = 0.050$
Proportion of seed crop dispersed	$F = 0.503$ $P = 0.687$ $R^2 = 0.040$	$F = 1.113$ $P = 0.397$ $R^2 = 0.200$
Number of viable seeds dispersed relative to the population average	$F = 36.27$ $P < 0.0001$ $R^2 = 0.824$	$F = 3.17$ $P = 0.061$ $R^2 = 0.018$

* These two groups of independent variables were identified by means of principal component analysis of the initial data set (see text). "Fecundity traits": plant size, final-sized fruit crop size, and % seeds viable. "Fruit-design traits": fruit diameter, seed dry mass, relative mass of dry pulp/fruit.

Discussion

The fleshy fruits of *P. lentiscus* provide an important food resource for most autumn-passage and wintering frugivorous birds in the lowlands of southwestern Spain. At the study site, at least 26 species eat the fruits and at least 19 are legitimate seed dispersers. The disperser coterie removed a great fraction of the fruit crop, most species depending to a great extent on the lipid-rich pulp for food. However, the mutual dependence relation was strongly asymmetrical since only four bird species accounted for 83% of removed seeds (see also Herrera 1984c, Jordano 1987c). The average percent removal of seeds was nearly identical in the two consecutive study years and showed very low inter-plant variability. However, individual plants showed very small between-year constancy in proportional removal but high constancy in the absolute numbers of viable seed removed, largely as a result of between-year constancy in fecundity for each plant.

It appears that seed dispersal in *P. lentiscus* is not severely limited by the interaction with seed dispersers. The necessary conditions to hypothesize a potentially great effect of avian dispersers on *P. lentiscus* fruiting traits are met: individual plants differing in dispersal-related traits show variation in fruit removal by birds, and these birds remove a great fraction of the realized reproductive output of the plant population in a given season. Thus, a relatively large number of species were recorded feeding on *P. lentiscus* fruits, and these fruits were a major element in their diets; percent removal was high and few fruits were taken by birds damaging pulp and/or seeds.

The net results of the interaction with mutualistic pollinators or seed dispersers may have direct consequences for the plant at two levels. First, fitness differences may exist if variation in flowering or fruiting traits has a direct influence on variation in the interaction. Phenotypic selection might follow and result in relevant demographic changes (Heithaus et al. 1982). Second, genetic response is required for this selective regime to be translated into differential perpetuation of the phenotypes (Endler 1986). The analysis of the seed dispersal system of *P. lentiscus* illustrates the kind of constraints that preclude adaptive change (*sensu stricto*) as a result of the interaction with mutualists (see Howe 1984, Herrera 1986, 1988, Wheelwright 1989). Thus, I found no evidence that variation in the percentage of the fruit crop removed by frugivores had direct effects on variation in relative fitness of different individuals. Additionally, if this direct effect actually exists, for example as a rare supra-annual event, it could hardly offset variation arising from both pollination constraints of the pre-dispersal phase and those imposed by the fertilization constraints that largely determine seed viability in the genus *Pistacia* and other Anacardiaceae (Grundwag 1976, Jordano 1988).

High percent removal of *P. lentiscus* seed are not

indicative of high dispersal of viable seed. Seed abortion and parthenocarpy (with no fruit shedding) are the main causes for this and result in very low actual removal of viable seed. Birds removed 82.5% and 83.3% of the final-sized fruit crop in the 1981–82 and 1982–83 seasons, respectively, but viable seeds removed actually represented only 23.2% and 37.6%, respectively, of this crop after correcting for the fraction of empty seeds in each season. The between-year difference in seed viability was the only factor responsible for this between-year difference in viable seed dispersed since other traits related to fruiting (e.g., crop size, phenology, removal by avian frugivores, fruit/seed predation levels) showed statistically insignificant variation in the two study seasons.

Reports of removal rates for Mediterranean fleshy-fruited plant species indicate that the figure estimated for viable seeds of *P. lentiscus* (i.e., the percentage of the initial fruit crop that the dispersed viable seeds account for) is among the lowest recorded (Herrera 1984c, Jordano 1984, Obeso 1986). Other studies showed that fruit removal might be very low due to the action of pulp/seed predators (e.g., Howe 1980, Davidar and Morton 1986, Piper 1986, Jordano 1987a), but few have examined if predispersal factors offset these late-acting factors in determining final variation in dispersed seed (see Heithaus et al. 1982, Herrera 1985b, 1988, Jordano 1987a, Krüsi and Debussche 1988). Variation in seed filling among *P. lentiscus* plants largely screens-off any variation in fruit removal attributable to the selective pattern of the frugivorous birds based on variation in fruit traits. Thus, the key-factor analysis showed that 'intrinsic' factors (embryo abortion, parthenocarpy, shedding of unpollinated flowers) caused far greater losses of seed than vertebrate and insect seed predation or ripe-fruit desiccation because of non-consumption by dispersers.

Fruit selectivity by legitimate dispersers of *P. lentiscus* resulted in dispersal of viable seed near the maximum possible for a given incidence of blank seed. Ripening is selective and is strongly associated with the presence of a fully-developed embryo. Since legitimate seed dispersers selectively ate ripe fruits, they predominantly dispersed viable seeds. Seed viability in a seed sample from faeces of the main disperser, *S. atricapilla*, doubled the recorded viability of seeds sampled from branches, suggesting that fruit foraging by the disperser was not random with respect to seed viability (actually fruit ripeness). Results of the preference experiments supported this, both for *S. atricapilla* and *E. rubecula*. Thus, the activity of seed dispersers resulted in a high probability that a fruit with a viable seed will be consumed by a legitimate disperser, in spite of the fact that these viable seeds represented a small fraction of the initial fruit crop.

Frugivore activity appeared to have a small effect, if any, on variation in fruit traits, largely as a result of its random variation with respect to phenotypic variation

in fruit traits. In addition, frugivore activity did not show a consistent variation with individual fecundity, either across the different individual plants or, for the same plant, in the two study seasons. Most authors agree that larger crop sizes do not necessarily result in increased removal (% crop consumed by frugivores) (see Howe and Smallwood 1982, Davidar and Morton 1986), and the corollary is that frugivore activity neither outweighs the initial differential in fecundity in the plant population, nor results in increased absolute seed dispersal of the more fecund individuals. As shown by the *P. lentiscus* data (see also Herrera 1988) the final contribution of each individual plant to the population seed production was largely determined at the pre-dispersal phase and the interaction with dispersers did not outweigh its net result.

Is there an adaptive reason for a high incidence of blank seed in *P. lentiscus* and *Pistacia* species in general? Excess production of final-sized fruits with inviable seed could increase attraction to frugivores and escape from seed predators (e.g., Janzen 1985). I found no evidence that plants with greater number of blank seed showed either increased percent removal or decreased damage levels by pulp/seed predators. Plants with greater numbers of inviable seed actually dispersed greater numbers of viable seed, but this was an indirect effect of the larger crop size, since seed viability showed no consistent relation with crop size. It would be conceptually erroneous to invoke adaptive explanations for variation in seed viability in *P. lentiscus* in the context of the seed removal phase, without considering that the proximate causes of variations in seed filling are related to the pollination process and, specifically, to the phase of fertilization and early growth of fruits (Grundwag 1975, Grundwag and Fahn 1969). Moreover, seed filling appears extremely variable and strongly associated to the specific circumstances experienced by each individual during pollination (Crane 1975, Jordano 1988). Seed inviability also shows a strong phylogenetic component, since similar patterns of seed abortion, parthenocarpy and pollination constraints have been described for other *Pistacia* species (Savastano 1926, Grundwag 1975, 1976).

Additional consideration must be given to the ancient origin of the genus *Pistacia*, with fossils undistinguishable from the living *P. lentiscus* recorded from the Oligocene in France (Zohary 1952). Thus, *P. lentiscus* is another member of an old Tertiary flora present in Mediterranean scrubland including taxa of tropical affinity (other Anacardiaceae, Lauraceae, Santalaceae, etc.) (see Suc 1984 and references therein) showing striking constancy of fruit traits over geological time. Thus, seed dispersal of *P. lentiscus* in ancient times should have been accomplished by a tropical African avifauna, quite different from the one I have described here, that existed in Europe during the mid-Tertiary period (Cracraft 1973). The present bird dispersers of *P. lentiscus* in the Mediterranean basin belong to genera

whose evolutionary centers are clearly Palaearctic and of recent origin (Snow 1978).

The interaction of *P. lentiscus* and its avian dispersers is thus largely driven by the consequences of its pre-dispersal biology. Pre-dispersal constraints derive from the pollination and fertilization patterns that show a strong phylogenetic component in the genus *Pistacia* as well as in other anacardiaceous species. Fruit traits of *P. lentiscus* appear as exaptations (i.e., characters that may have a "contemporary" effect on fitness but were not selected for their current role, Gould and Vrba 1982) with little, if any, direct effects on variation in seed removal by the frugivores that are its present-day seed dispersers. Variation in the percentage of the fruit crop removed by frugivores did not outweigh the strong effects that plant size, number of final-sized fruits and percent seed viability had on estimates of seed dispersal relevant to fitness.

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