

## Weak interactions between avian and insect frugivores: the case of *Pistacia terebinthus* L. (Anacardiaceae)

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### Abstract

Vertebrate frugivores often feed on fruits upon or within which insects also feed, yet little information exists on the potential magnitude of interactions between these consumers. The Mediterranean shrub *Pistacia terebinthus*, the birds that consume its fruits, and the wasps that feed upon its seeds are examined in this study.

*P. terebinthus* produces a highly variable fraction of final-sized red fruits that never become mature (green-colored). Red fruits can be immature, parthenocarpic, aborted, or attacked by wasps, and their pulp is much less nutritious than that of mature fruits. A total of 20 bird species consumed the fruits in the study area. Legitimate dispersers accounted for 39% of the total fruit removal, while pulp eaters and seed predators accounted for the remainder. Birds strongly preferred the mature fruits (only 4% of the fruits consumed were red). The incidence of wasps in the seeds ranged from 0 to 42% of the crop in 1989 and from 0 to 24% in 1990. The influence of avian and insect frugivore guilds on each other appears to be quite low because of the narrow overlap in resource utilization by birds and wasps, and an overall low intensity of wasp seed predation. From an evolutionary perspective, the possible ability of wasps to preclude fruit maturation appears not to be attributable to the present interaction with avian frugivores.

### Introduction

Vertebrate frugivores and insects often feed on the same fruits, either on the pulp or the seeds. The possible interaction between these two guilds of consumers has been explored by relatively few studies compared to those on both the plant-seed disperser mutualism and the plant-insect parasitic relationship. Such an interaction may affect insect population dynamics (Bigler & Delucchi 1981; Janzen 1982; Herrera 1984a, 1989; Drew 1987), and/or the vertebrate's choice of fruits (Manzur & Courtney 1984; Redford *et al.* 1984;

Bauer 1986; Jordano 1987; Burger 1987; Borowicz 1988; Semel & Andersen 1988; Krischik *et al.* 1989; Valburg 1992a, b). In either case, there should be important consequences for seed dispersal (see Manzur & Courtney 1984; Jordano 1987).

Besides decreasing the resources available to the insects, vertebrates may kill any developing insect inside the ingested fruit (cf. Lamprey *et al.* 1974; Halevy 1974). It is generally assumed that insect and vertebrate frugivores compete in a 'race' (Janzen 1976) that results in selection against those insects that oviposit late enough in

fruit maturation that larval development overlaps with vertebrate fruit consumption. The studies by Bigler & Delucchi (1981) and Drew (1987) suggest that vertebrates are the major natural enemies of tephritid flies that feed on fruit pulp. The fact that larvae leave the fruits to pupate in the soil may be an adaptation to escape from being eaten by vertebrates (Drew 1987). In the case of insect seed predators, however, there is no substantial evidence that vertebrate frugivory represents a major insect mortality factor (but see Lamprey *et al.* 1974; Halevy 1974; Herrera 1989a).

The goal of the present study is to examine the interaction between avian frugivores and the insect seed predators of the Mediterranean shrub *Pistacia terebinthus* (Anacardiaceae). The bird species that consume the fruits in the study area and the insect species that prey upon the seeds of this plant were identified. Next, the variability in both seed predation by insects and avian frugivory was examined, in relation to plant traits, in order to assess the overlap in fruit utilization. In this way it should also be possible to determine whether plant traits selected by the avian frugivores coincide with those selected against by the insect seed predators.

#### Study site

The study was carried out at Parque Natural de Cazorla, Segura y Las Villas, eastern Andalucía (southeastern Spain), during the fall of 1989 and 1990. Descriptions of the Sierra de Cazorla, a mountain chain 40 km long with a maximum elevation of 2107 m, can be found in Fernández Galiano & Heywood (1960), Polunin & Smythies (1973: 83–89) and Otero *et al.* (1978). One of the study sites (Agracea) is located between 1100 and 1200 m in the Guadahornillos Valley. This site is occupied by dense Mediterranean forest constituted mainly by *Quercus*, *Phillyrea*, *Arbutus* and *Juniperus*. Here *Pistacia terebinthus* usually grows in small gaps or along trails, and its density is rather low (1–15 individuals/ha). The other study site (Las Navillas) is located about 5 km of the

small town of Vadillo-Castril, at an altitude of approximately 1000 m. This site is a large secondary scrub, which until recently was intensively used for sheep and goat grazing. The terrain is calcareous and very rocky, and *P. terebinthus*, *Quercus rotundifolia*, and *Pinus pinaster* are the commonest vegetation. Additional observations were made on *P. terebinthus* shrubs located on the road from Puente de las Herrerías to the source of the Guadalquivir River.

Mean annual precipitation at Vadillo-Castril, the nearest weather station, is 1201 mm (the range for 26 years is 669–1970 mm; Herrera 1991). In the two years of the study, rainfall was 916.5 mm and 553.0 mm., respectively. The summer (from June to mid-September) is dry. Snowfalls are frequent from November to March, although at the altitudes where *P. terebinthus* lives snow does not remain longer than a week or two. Mean monthly temperatures of the coldest (January) and hottest (August) months are 4.0 °C and 21.1 °C (Herrera 1991).

#### Study organisms

*P. terebinthus* is a dioecious woody shrub or small tree that can reach a height of 10 m. It is distributed around the Mediterranean from Portugal to Turkey and from Morocco to Cyrenaica, as far as the southern Alps (Zohary 1952). Flowering occurs towards the end of April, just preceding leaf growth, and lasts until the beginning of June. Inflorescences of 3- ca. 50 anemophilous flowers are always grouped in panicles. A panicle may contain up to 20 inflorescences and up to 800 flowers, although the usual is 100–400 flowers. Single branches may contain up to 10 panicles, usually quite close to each other and at the distal end of the branch. Males tend to start flowering somewhat earlier than females.

After anthesis, the ovary – but not the ovule – grows continuously until reaching its maximum size about a month later. One or two weeks later, the endocarp becomes woody. Along with the endocarp, the pericarp also develops before and independently of the ovule (or embryo if it has

been fertilized). As in other species of *Pistacia* (Grundwag 1976), there is probably a delay in syngamy (Grundwag & Fahn 1969), the fertilized ovule reaching its final size several months after anthesis.

The fruit is a drupe measuring  $6.6 \pm 0.07$  (s.d.) mm long and  $5.9 \pm 0.7$  mm wide ( $N = 575$ ). A viable seed fills the entire fruit locule with a green endosperm. Fruits lacking viable seeds are either parthenocarpic, i.e. come from unpollinated flowers (showing vestiges of funiculus and ovule), or are the result of embryo abortions, which can occur at different stages of development. In late abortion, the small seed may contain some endosperm, but this never occupies the entire fruit locule. Detailed information on the causes of these types of seeds can be found in Grundwag & Fahn (1969), Grundwag (1975, 1976) and Crane (1975). Mature, green fruits have an average weight of  $0.14 \pm 0.03$  g ( $N = 147$ ), which is significantly higher ( $r = 0.89$ ,  $DF = 278$ ,  $F = 75.62$ ,  $P = 0.0001$ ; 10 plants) than that of inviable red fruits ( $0.09 \pm 0.02$  g;  $N = 150$ ). Viable seeds weigh  $0.05 \pm 0.01$  g ( $N = 147$ ).

Final-sized fruits with inviable seeds are retained on the plant for several months. Whole infructescences usually start falling by mid-end October, before fruits have become desiccated. Immature fruits are red and become green or bluish green after maturation. Fruits with inviable seeds are indistinguishable from immature viable fruits. As found in *P. lentiscus* (Jordano 1989), fruit ripening is strongly associated with seed viability. Of a total of 3700 fruits dissected in 1989, only a small proportion (1.5%) had an apparently viable seed but did not become mature. Except on six occasions in which seeds had been damaged by larvae, all the dissected green fruits ( $N = 705$ ) contained viable seeds.

Chemical analyses of the pulp of both ripe and red fruits indicated that they differed considerably in lipid content ( $35.83 \pm 8.65\%$  vs.  $3.92 \pm 1.61\%$ , respectively). Quantities of all other compounds except calcium were similar in the two types of fruits. The amount of calcium appeared to be significantly higher in red ( $0.30 \pm 0.04$ ) than in green fruits ( $0.16 \pm 0.05\%$ ) ( $P < 0.05$ ; Mann-

Whitney test). The procedures of the chemical analyses are described in detail in Herrera (1987).

Four species of chalcidoid wasps emerge from the seeds of *P. terebinthus*. The most common species are *Sycophila* sp. and *Megastigmus pistaceae* Walker 1871. The two other species, *Cyrtoptix* sp. and *Eurytoma* sp. (in the *pistaciae* group) are rarely found and might be parasitoids of *M. pistaciae* (Davatchi 1956). *M. pistaciae* and *Sycophila* sp. overwinter as larvae and emerge as first-generation adults in late June or early July, when the fruits of *P. terebinthus* are already full-sized and have a woody endocarp. Adult females probably lay only one egg within each fruit because seeds bear a single larva, although on one occasion two larvae were found in the same fruit. Attacked fruits remain red and resemble intact ones. Pupation occurs within the fruits, and adults emerge beginning in mid-August. Thus, wasp developmental time takes about 40–50 days, as found by Davatchi (1956) in *P. vera*. The adult females of this second generation oviposit on the fruits still on shrubs and their offspring spend the winter as larvae. The other species, *Sycophila* sp., emerges at the same time as *M. pistaciae* and has a similar developmental time. However, *Sycophila* sp. probably has three generations per year, since adults emerge as late as mid October, and females have been seen ovipositing on the fruits at this time.

The fruits are consumed by a variety of birds, some of which are migratory. Ants have sometimes been seen feeding on the ripe pulp of fruits on the shrub, and they also take fallen fruits to their nests. Carnivores, mainly the red fox (*Vulpes vulpes*), may also consume fallen fruits; they act as seed predators since seeds appear broken in their faeces (Herrera 1989b). The field mouse, *Apodemus sylvaticus*, also eats fruits, as evidenced by broken seeds often found below fruiting shrubs.

## Methods

The fruit ripening phenology of 158 marked female plants (120 from Las Navillas and 38 from

Agracea) was determined in 1990 by visiting the plants every 3–5 days and recording the proportion of mature fruits in the entire plant. From twenty-eight of these plants, a sample of 50 fruits per plant was dissected in order to determine the proportion of viable seeds and the incidence of wasp seed predation. Aborted fruits were distinguished from parthenocarpic ones by the presence of a more or less enlarged embryo. Fruit crop size, plant height, canopy diameter, and distance to the nearest two neighbors were measured for each plant. Fruit crop size was estimated by complete count of the final-sized fruits. Average fruit diameter was obtained by measuring 25 fruits from each plant (red and green fruits are of similar size). Preliminary data on the incidence of insect-damaged fruits were gathered in 1989 from a sample of 50 fruits of each of 74 plants (20 from Agracea, 25 from Las Navillas, and 29 from along the road to the Guadalquivir source).

In order to determine fruit choice by birds and their intensity of fruit removal, five fruit panicles per plant from a sample of 18 plants were randomly chosen and marked during the ripening period of 1990. The total number of final-sized fruits was counted for each panicle before fruit removal by birds began. Fruits were again counted every 3–5 days until all mature fruits disappeared and most immature fruits began falling. A set of four fruit traps (40 × 40 × 6 cm) were placed beneath each canopy to collect the falling mature fruits. These traps were under about 2/3 of the total number of mature fruits produced. Thus, the total number of mature fruits dropped was estimated as one and a half times the number of fruits in the traps and subtracted from the total number of mature fruits that disappeared. Red fruits are much more strongly attached to the branches than mature fruits and do not easily fall unless they are completely dry. Usually, the whole infructescence containing red fruits dries out and falls (most mature fruits have been removed by this time). The number of fruits that began drying out was recorded in each census, and was not considered as removed by birds in the following census. Mature fruits can remain on the plant for several weeks before drying.

Direct observations on bird visitation and fruit removal were made on another 18 plants. Plants were observed for 13 days from October 16 to November 4 1990, between 8:30 am to 6:30 pm. All 18 plants were observed at randomly selected times each day for 30 minutes. Previous observations on some of those and other plants were made after September 21, mainly to learn the species that visited the plants. Total time spent in the direct observations was 163.25 h. For each bird visit to a plant I recorded the species, whether it fed on fruits, the color of the fruits removed, and the total number of fruits removed.

In order to determine whether the number of bird visits and the proportion of fruits removed was associated to some plant trait, I measured the following variables for each plant: fruit crop size, proportion of fruits maturing, plant height, canopy diameter, number of fruiting conspecific individuals within a 10 m radius, and foliage density (high, low, or intermediate). In addition, the distances to the crowns of all trees or shrubs of any species along four perpendicular transects 10 m in length were averaged. The first transect was always taken to the nearest tree or shrub. This value, here called the degree of isolation of the plant, expresses the average minimum amount of open country a bird had to cross to reach it from another perch.

Fruit preferences were tested also on caged individuals of *Sylvia atricapilla* (N = 4), *Parus caeruleus* (N = 3), *Parus ater* (N = 1) and *Parus major* (N = 1), the main fruit consumers of *P. terebinthus*. Additional trials were run for two more species (*Parus cristatus* and *Erithacus rubecula*), but these failed because the birds refused to eat in captivity. Three different trials were run (when possible) for each individual bird and involved presenting infructescences with different proportions of mature fruits to the bird in random order: a) 30 red and 30 green, b) 40 red and 20 green, and c) 60 red and 0 green. During each trial, which lasted 20 min, I recorded the bird's choice and the number of fruits consumed.

All statistical analyses were performed using SAS (1985). Percentages and proportions in the ANOVAs and multiple regressions were arcsine

transformed. Both Spearman and Pearson correlations were used and are distinguished in the results section as ( $r_s$ ) and ( $r$ ), respectively. Standard deviations are given with the means throughout the paper.

## Results

### *Fruiting and ripening patterns*

The average fruit crop in the plants observed in 1989 was  $1,542 \pm 1,401$  fruits (range 150–6,230;  $N = 45$ ), and the proportion of the fruit crop that ripened averaged  $13.1 \pm 14.9\%$  (range 0–54%;  $N = 45$ ). In plants that yielded mature fruits this average was  $17.82 \pm 14.73\%$  ( $N = 33$ ). Of the 120 female plants marked and monitored in Las Navillas area in 1990, 30 (25%) produced no mature fruits at all. The other 90 plants ripened from 1 to about 75% of their fruit crop, the average being  $16.1 \pm 19.2\%$  (Fig. 1). Mean fruit crop size was  $2,073 \pm 3,579$  (range 3–20,000;  $N = 120$ ), whereas number of ripe fruits averaged  $686 \pm 1,732$  (range 0–11,500;  $N = 120$ ). In the Agracea area, with similar fruit crop sizes, only 3 of 38 plants (8%) yielded some mature fruits.

Figure 2 shows the fruit ripening phenology in a haphazardly chosen sample of 18 individuals observed in 1990. Data on fruit ripening phenology were not available for 1989. The fruit ripen-

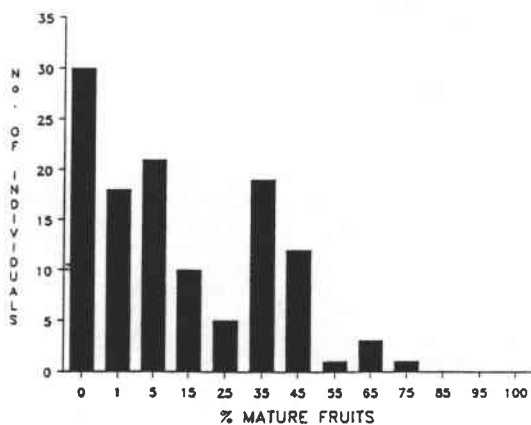


Fig. 1. Frequency distribution of plants with a given proportion of mature fruits in the total crop. Data from 1990.

ing period in a single individual lasted an average of  $45 \pm 8$  days, ranging from 30 to 57 days. By mid September, almost all plants had ripened the fruits, but these remained on the branches for several weeks before they were removed by birds.

Most inviable seeds of *P. terebinthus* were the result of embryo abortions ( $37.8 \pm 16.3\%$ ;  $N = 74$  plants in 1989;  $70.1 \pm 13.1\%$ ,  $N = 28$  plants in 1990), although parthenocarpy was also important ( $30.7 \pm 15.8\%$ ,  $N = 74$  in 1989;  $17.7 \pm 13.9\%$ ,  $N = 28$  in 1990). The proportion of embryo abortion and parthenocarpy was similar at all study sites (Table 1). A detailed account of the intra- and inter-population variation in the production of aborted and parthenocarpic fruits will be published elsewhere (Traveset, in prep.). Greater pollen limitation in 1989 (mainly because of rains during the flowering period) was apparently the cause of the higher parthenocarpy that year.

### *Seed predation by chalcidoid wasps*

The average percentage of the fruit crop attacked by wasps in 1989 was  $11.0 \pm 9.9$  (range 0–42%;  $N = 74$  plants). In 1990, that percentage averaged  $4.6 \pm 6.3$  (range 0–24%;  $N = 28$  plants) (Fig. 3). In 16.2% of the plants from which fruits were collected in 1989 no fruits were found to be damaged by wasps. That value doubled in 1990; 9 of the 28 plants (32.1%) showed no evidence of insect seed predation. There might be some consistency between years in the incidence of wasps in an individual plant since at least four plants of the seven studied in both years had a similar proportion of insect damaged seeds. However, more data are needed to test this possibility.

In 1989, the proportion of attacked fruits per shrub varied significantly among areas ( $r = 0.43$ , ANOVA,  $DF = 73$ ,  $F = 7.94$ ,  $P < 0.001$ ), the highest occurring in Las Navillas, where *P. terebinthus* occurs at high density, and the lowest in the Agracea, where the species is less common (Table 1). The incidence of wasp seed predation was neither correlated with crop size ( $r_s = 0.03$ ,  $P > 0.05$ ) nor to fruit dimensions (length or diameter) ( $r_s = 0.18$  and  $r_s = 0.16$ ,  $P > 0.05$ , respectively).

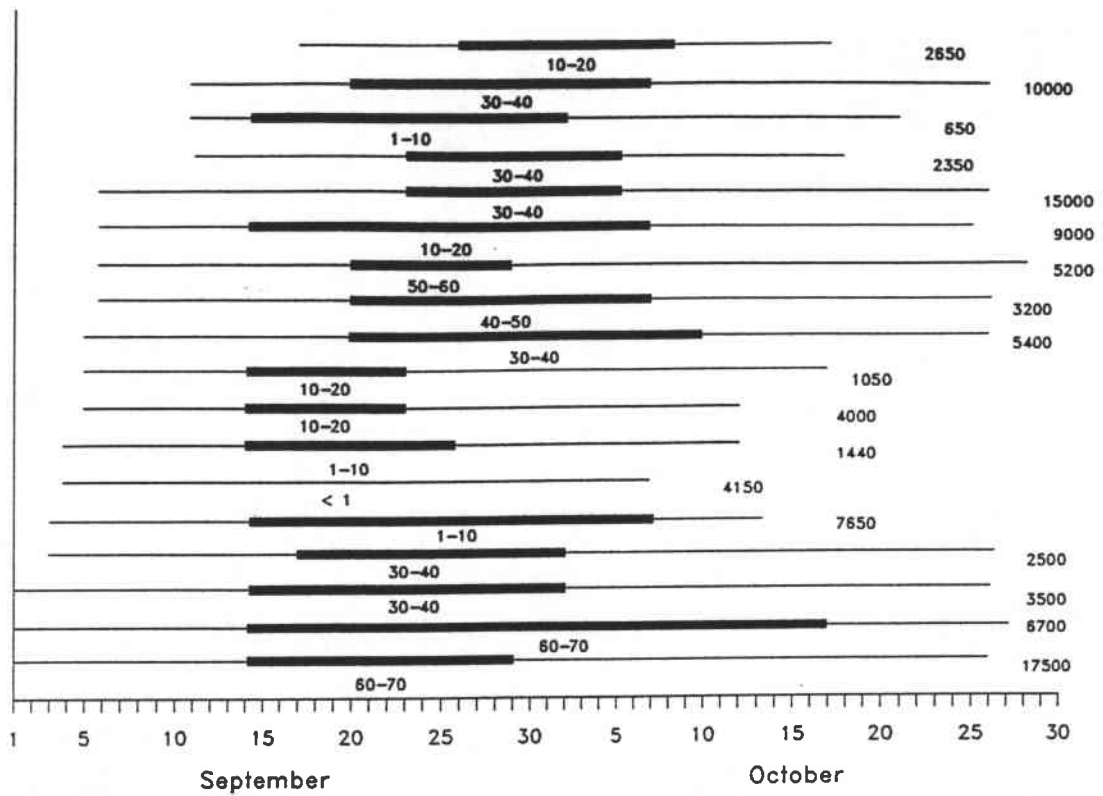


Fig. 2. Fruit ripening phenology of 18 selected individual plants in 1990. Each line represents the entire period of ripe fruit availability. The filled bars indicate the period during which the maximum percentage of mature fruits was available. This percentage was estimated visually a 10% intervals and is indicated under the bars. The numbers to the right of each line stand for total crop size.

In contrast to the results obtained in 1989, the proportion of damaged seeds at Las Navillas was not significantly different ( $r = 0.12$ ,  $DF = 27$ ,  $F = 0.39$ ,  $P > 0.05$ ) from that at the Agracea area (Table 1). These results suggest that plant density

does not consistently determine the incidence of wasp seed predation each year.

The proportion of seeds attacked by wasps appeared to be significantly correlated with only fruit crop size ( $r = 0.53$ ,  $P < 0.01$ ) and not with any of

Table 1. Percentages of parthenocarpic, aborted, wasp-attacked, and mature fruits from the plants studied in 1989 and in 1990 in the different areas. Figures are means and standard deviations.

Area	N	Parthenocarpic	Aborted	Wasp-attacked	Mature
1989					
Navillas	20	33.4 ± 11.0	30.8 ± 11.3	15.4 ± 10.0	18.6 ± 15.0
Agracea	25	36.3 ± 20.0	50.0 ± 14.3	5.1 ± 5.7	6.2 ± 11.8
Guadalq.	29	24.5 ± 14.5	35.4 ± 16.9	11.2 ± 10.1	28.3 ± 16.5
1990					
Navillas	15	16.4 ± 15.4	67.3 ± 16.4	3.9 ± 6.1	12.3 ± 12.5
Agracea	13	19.2 ± 12.2	73.2 ± 7.2	5.4 ± 6.7	2.2 ± 4.2

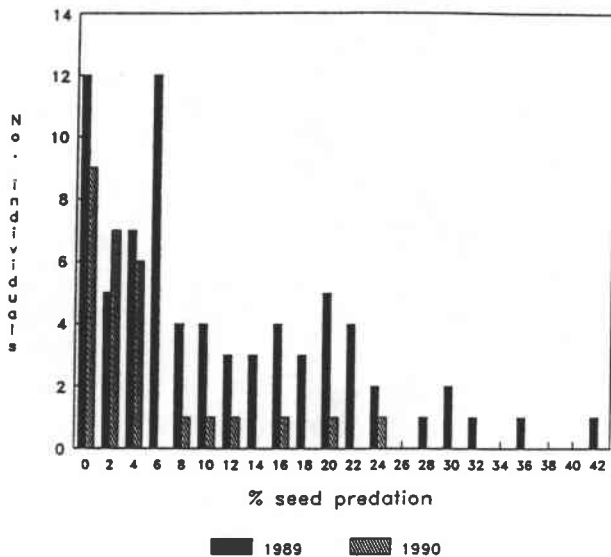


Fig. 3. Frequency distribution of individual plants with a given percentage of their total seed crop attacked by chalcidoid wasps in the two years of study. Notice the large number of plants lacking fruit damage by insects. A total of 50 seeds were examined per plant.

the other variables measured for each plant in 1990 (plant height, canopy diameter, fruit diameter, average distance to the two nearest fruiting neighbors, and number of fruiting conspecifics in a 10 m radius). The proportion of attacked seeds was not correlated to that of parthenocarpic, aborted or mature fruits, either. Wasp larvae are able to survive in seeds that are not full-sized yet. Fruit dissections showed that the seeds from which adults had emerged usually filled less than 50% of the fruit locule. At least the first generation of both *Megastigmus pistaciae* and *Sycophila* sp. had to develop in seeds that were not full-sized, since all adults have emerged by late August, and at this time seed development is not complete yet. The second generation of *Sycophila* emerges by late September, when seeds are already full-sized. However, even at this time it is not uncommon to find larvae living in undeveloped seeds, suggesting that (1) larvae have enough endosperm to feed on in late-aborted seeds, and/or (2) larvae prevent full seed development once they start feeding.

During September and October, *Sycophila* was observed only on red fruits, even on those plants

with a high proportion of green fruits on them. So far, it is unknown whether wasps can discriminate between red fruits with empty seeds from those with some endosperm inside. In order to increase their offspring survival during winter, it seems that adults should be able to choose for oviposition those fruits containing seeds with larger amounts of food.

*Fruit consumption by frugivorous birds*

*a) Indirect observations of fruit removal*

Percent removal of green fruits by birds averaged  $98.8 \pm 2.9\%$  (range 88.2–100%). Birds did not leave a single ripe fruit in 14 of the 18 plants monitored in Las Navillas. These values contrast strongly with the  $2.7 \pm 3.4\%$  removal of red (inviable) fruits (range 0–13.2%). Fig. 4 shows the

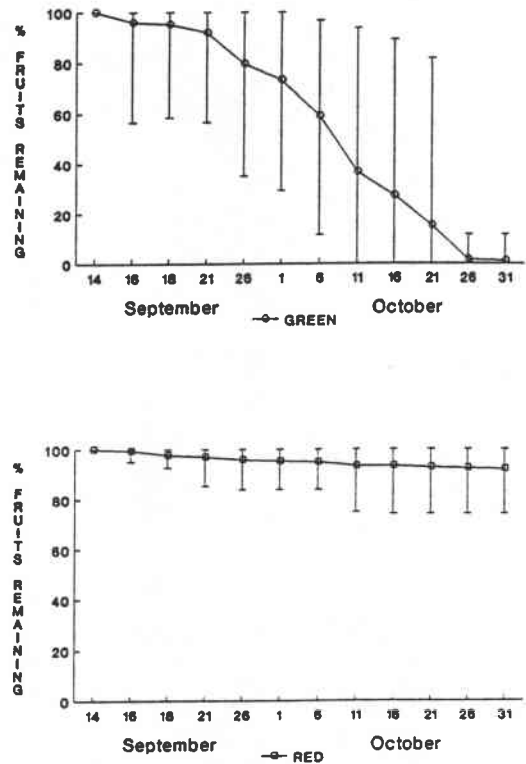


Fig. 4. Removal of green (mature) and red (immature) fruits by birds from 18 selected plants. Vertical bars indicate standard deviations around means. Notice the decline in green fruits coinciding with the arrival of migrant frugivores.

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2.2 ± 4.2

average removal rates of red and green fruits from the beginning to the end of the ripening period. Fruit removal rate increased towards the end of September, and coincided with the arrival of migratory birds. On October 21, 77.8% of the plants still had some green fruit on their branches; by October 26 this figure had dropped to 33.4%. The time during which ripe fruits were consumed varied between 25 and 47 days, with an average of  $39 \pm 6$  days. In a correlation analysis, the duration of this period was not associated to any of the variables measured from each plant.

Red fruits were removed simultaneously with the ripe ones, not after the latter had been depleted. In only two plants did the highest proportion of red fruit removal occur after all green fruits had been consumed. After the ripe fruits of most plants in an area were exhausted, birds appeared to leave the area, and soon thereafter entire infrutescences of red fruits began to fall off.

Percent removal of red fruits (those that may contain wasp larvae inside) was significantly correlated with fruit crop size ( $r_s = 0.68$ ,  $P < 0.01$ ) and with the average distance to the two nearest fruiting neighbors ( $r_s = 0.60$ ,  $P < 0.01$ ). In a multiple regression analysis, these two variables explained 59% of the variation in percent removal of red fruits, although the effect of the second was not significant ( $P = 0.07$ ). Fruit crop size, thus, appears to be a good predictor (explaining 52% of the variance) of the proportion of red fruits removed by birds.

Neither the proportion nor the absolute number of red fruits removed was related to the proportion or the absolute number of fruits attacked by wasps in a correlation analysis. Damaged fruits apparently look like the undamaged ones, and it seems unlikely that birds can distinguish between them. There was also no correlation between the proportion of either red or green fruits removed by birds and the other plant variables measured – height, canopy diameter, or average fruit diameter –.

#### b) Direct observations of fruit removal

A total of 20 bird species was recorded as fruit consumers of *Pistacia terebinthus* in the study

areas (Table 2). Ten of these species are legitimate seed dispersers and represented 37.5% of the total number of visits to the fruiting trees. Five species of pulp consumers and five of seed predators accounted for the remainder (47.6% and 14.9%, respectively).

Not all plants were equally visited by all species (Fig. 5). Some attracted mostly pulp consumers while others were visited mainly by legitimate dispersers. The proportions of visits by these two types of frugivores were negatively correlated ( $r_s = -0.83$ ,  $P = 0.0001$ ). Seed predators, on the other hand, were seen in most (72%) plants and their visits were not correlated with those by other frugivores. Plant isolation appeared to determine, in part, the type of visiting frugivore: the more isolated (with little vegetation cover nearby) the plant, the higher the probability of being vis-

Table 2. Avian frugivores that consumed *Pistacia terebinthus* fruits and total number of visits to the fruiting plants during observations in 1990. *Garrulus glandarius* was observed visiting shrubs twice but it is not included in the table because its feeding type on this plant is unknown. Most observations come from Las Navillas.

Feeding type	Bird species	Number of visits
Pulp consumers	<i>Parus ater</i>	191
	<i>Parus major</i>	99
	<i>Parus caeruleus</i>	184
	<i>Parus cristatus</i>	30
	<i>Aegithalos caudatus</i>	55
Seed dispersers	<i>Sylvia atricapilla</i>	211
	<i>Sylvia melanocephala</i>	15
	<i>Sylvia communis</i>	1
	<i>Phoenicurus phoenicurus</i>	32
	<i>Phoenicurus ochruros</i>	93
	<i>Erithacus rubecula</i>	84
	<i>Turdus philomelos</i>	1
	<i>Turdus merula</i>	2
	<i>Ficedula hypoleuca</i>	1
<i>Corvus corone</i>	1	
Seed predators	<i>Sitta europaea</i>	29
	<i>Fringilla coelebs</i>	114
	<i>Dendrocopos major</i>	7
	<i>Carduelis chloris</i>	13
	<i>Coccothraustes coccothraustes</i>	12



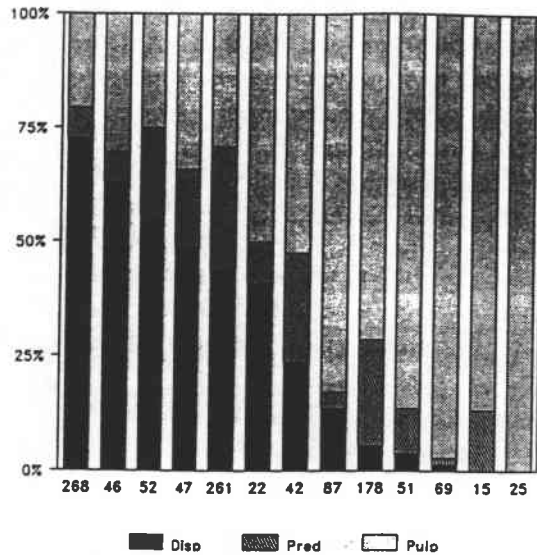


Fig. 5. Proportion of visits by legitimate dispersers (Disp), seed predators (Pred) and pulp eaters (Pulp) in 13 plants. Not included are five plants that received less than three visits. Numbers at the bottom indicate the total number of visits to each plant. Notice the negative correlation between visits by dispersers and by pulp eaters, reflecting differences in the habitat preferences of the two avian guilds.

ited by a pulp consumer ( $r_s = 0.78$ ,  $P = 0.0015$ ;  $N = 13$  plants). In contrast, plants with more available perches and nearby cover were more frequently visited by either legitimate dispersers or seed predators ( $r_s = -0.68$ ,  $P = 0.01$  and  $r_s = -0.70$ ,  $P = 0.08$ , respectively;  $N = 13$  plants). Proportion of visits by a particular type of frugivore was not correlated with plant size, crop size, absolute number of ripe fruits, foliage density, distance to the two nearest fruiting conspecifics, or number of fruiting conspecifics in a 10 m radius.

Considering only feeding visits, 96.1% of the fruits removed ( $N = 877$  fruits) were green whereas only 3.9% were red (Table 3). Legitimate dispersers accounted for 39.1% of fruit removal (0.5 and 38.7% of red and green fruits, respectively); the other 60.9% of the fruits were taken by either pulp consumers or seed predators.

Legitimate dispersers, in particular *S. atricapilla* and *E. rubecula*, accounted for only four of the 34 red fruits consumed. Six red fruits were taken by pulp consumers (*P. ater*, *P. major* and *A. cau-*

Table 3. Consumption of fruits by birds during feeding observations in 18 plants. Numbers in parentheses represent the percentages of total fruit consumption.

Type of frugivore	Red fruits	Green fruits
Legitimate dispersers	4 (0.5)	339 (38.7)
Pulp eaters	6 (0.7)	372 (42.4)
Seed predators	24 (2.7)	132 (15.1)

*datus*) while the remaining 24 were removed by seed predators, particularly, by *C. chloris*. In two occasions, *C. coccothraustes* was observed cutting infructescences with red fruits and rejecting them to reach the green ones.

The proportion of ripe fruits consumed by legitimate dispersers was negatively correlated with that consumed by pulp or seed eaters ( $r_s = -0.99$ ,  $P = 0.0001$ ;  $N = 11$ ). That is, some plants had their fruits eaten mostly by legitimate dispersers while in other plants it was mostly other birds. It was also negatively correlated with the degree of plant isolation, although not significantly ( $r_s = -0.20$ ,  $P > 0.05$ ). In contrast, the proportion of ripe fruits consumed by non-legitimate dispersers was positively associated with plant isolation ( $r_s = 0.21$ ,  $p < 0.005$ ). There were no significant correlations between the proportion of red or green fruits consumed by either kind of birds and the variables measured for each plant (including proportion of fruits that ripened).

The nine caged individuals of the four species tested did not show any interest in red fruits. When offered the two different mixtures of green and red fruits they consumed only green ones; when offered only red fruits they did not eat. Three individuals (two males and one female) of *Sylvia atricapilla* were forced to eat red fruits with wasp larvae inside. The fruits ( $N = 3$ ) were defecated within 30 and 75 minutes; they still contained much pulp, and the larvae appeared intact.

## Discussion

*Pistacia terebinthus* is one of the Mediterranean plants whose fruits represent a rich food resource