ספרית אורנים

המאמרים במועברת הדפסיםוזמונועל-פי
חוק 2 בודיקאיצרי

הדפסת מאמרים текיתעהזרילימודוהוראהבלבד

איןلعשותכלשמותמסחרבמאמרים.
THE RELATIONSHIPS BETWEEN FRUIT RIPENESS, WASP SEED PREDATION, AND AVIAN FRUIT REMOVAL IN PISTACIA PALAESTINA

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ABSTRACT

Substantial variation in fruit removal between individual Pistacia palaeantina plants was observed in northern Israel. To elucidate the causes of this variation, I examined several proximal sources of between-individual variation in fruit removal and dispersion efficiency. Crop size, tree height, and diameter explained some between-individual variation in fruit removal. Dispersal efficiency was mainly influenced by the proportion of the unripe fruits (including aborted and parthenocarpic fruits). Comparison of several reproductive parameters of P. palaeantina with another Pistacia species (P. terebinthus) in Spain, revealed that P. palaeantina produces larger fruit crop, faces higher seed predation by infesting wasps, and has lower proportions of parthenocarpic and fruit abortion than Pistacia terebinthus. Fruit removal and dispersal efficiency of the former is much higher than the latter.

INTRODUCTION

The reproductive output of a bird-dispersed plant in the form of dispersed seeds might be a consequence of the simultaneous interactions between the plant, its avian seed dispersers, and its frugivorous insects (e.g., Herrera, 1984a,b; Jordano, 1989; Traveset, 1993a, 1994b).

Parthenocarpy, the production of fruits without viable seeds, is a widespread phenomenon in different plant families such as Anacardiaceae. The main cause for parthenocarpy is pollination failure. Yet, the plants produce, maintain, and further develop such fruits. Therefore, an interesting evolutionary question arises: why do plants invest resources in infertile fruits? One possible kind of answer might be that there is no adaptive value in producing parthenocarpic fruits. Willson and Burley (1983) suggested that (a) fruit development is not resource limited and (b) parthenocarpy is a "mistake". However, they also suggested an adaptive explanation in that parthenocarpy can serve to reduce herbivorous damage.

Zangerl and Berenbaum (1991) demonstrated that parthenocarpic fruits in Pastinaca sativa may act as decoys that divert herbivorous insects away from fertile fruits. Traveset (1993a,b) also found that parthenocarpic reduced wasp seed predation in Pistacia terebinthus. However, while the former study explained this phenomenon by higher absolute content of secondary compounds in seedless fruits, the latter suggested that wasps cannot discriminate between viable and not viable fruits. Therefore, they may oviposit by mistake in seedless fruits which are not suitable for larval development.

Another adaptive explanation to the production of infertile fruits might be related to their role in attracting frugivorous birds by acting as "flags" (Willson and Thompson, 1982; Willson and Whelan, 1990). Recently, the "flag" theory was experimentally examined in P. terebinthus by Fuentes (1995). He showed that although the infertile fruits apparently attract frugivores, they also act as a barrier that interferes with the access of these birds to the ripe fruits and therefore prevents them from dispersing seeds.

The aims of this study were (1) to document for the first time the extent of parthenocarpy and wasp seed predation in P. palaeantina, (2) to correlate dispersal success with parthenocarpy and seed predation, and (3) to compare several reproductive parameters of P. palaeantina with the closely related P. terebinthus.

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METHODS

NATURAL HISTORY OF THE ORGANISMS

Pistacia palaestina (Anacardiaceae) is a deciduous tree or shrub, widespread in the eastern Mediterranean region, from Turkey to Israel, where it is one of the most important associates of Quercus calliprinos and of other forest and maquis formations (Zohary, 1952). P. palaestina is very closely related to Pistacia terebinthus but Zohary (1952) gave some evidence to justify Boissier who assigned P. palaestina a specific rank. The distribution area of P. terebinthus is in the western Mediterranean region from Portugal to Turkey, thus the distribution area of P. palaestina is exclusive of P. terebinthus in Southern Turkey, Syria, Lebanon, and Israel (Zohary, 1952).

The fruit is a drupe, 5–6 mm long, 4–5 mm broad (Zohary 1952) with wet pulp mass:wet seed mass ratio of 1.05 (Izhaki, 1986). In comparison to other fruit-bearing plants in the eastern Mediterranean region, the proportion of fats and protein in its pulp are relatively high (57.8% and 7.1% of dry mass, respectively) while the proportions of carbohydrates and water are relatively low (12.4% dry mass and 43.8% wet mass, respectively). This pulp is also one of the most energy-rich sources found in this ecosystem (28.06 kJ per 1 g dry matter, Izhaki, 1986). The unripe fruit are pink-red while ripe fruit are bluish. Fruit ripening begins in August and ripe fruit can be found until the end of October.

As was detected in this and other Pistacia species (e.g., Izhaki, 1986; Jordan, 1989) the final fruit does not necessarily include a viable seed. As observed earlier in P. lentiscus (Jordan, 1989) and P. terebinthus (Traveset, 1994b), fruit ripening is strongly associated with seed viability: while the color of the fruits with empty seeds remain pink-red, those with viable seeds become bluish. The fruits with empty seeds are not immediately abscised but remain on the plant at least until the disappearance of the fruits with viable seeds (Izhaki, 1986). The pulp of fruits with empty seeds contain much less fats (13.5%) than that of fruits with viable seeds.

Three different mechanisms may cause Pistacia fruits to remain unripe in the pink-red phase, yielding only inviable seeds: parthenocarpy due to unpollinated flowers, embryo abortion, and seed predation by wasps.

The chalced wasp Eurytoma plotkovi deposits eggs in Pistacia fruits. Hatched wasp larvae move within the host seed and kill the embryo. Larvae hibernate in the host fruit and the adults emerge in July–August by cutting a hole in the pulp. Attacked fruits remain red and resemble intact fruits.

In contrast to observations in P. terebinthus in Spain (Traveset, 1994a), P. palaestina in the eastern Mediterranean scrubland in the Judean Hills (100 km southeast of the present study site) was mainly consumed by legitimate dispersers, mainly frugivorous birds, and only marginal activity of pulp eaters and seed predators was observed (Izhaki, 1986). Among the six frugivorous birds that consumed P. palaestina fruits in Judean Hills, five were transients (Sylvia atricapilla, S. hortensis, S. curruca, S. borin, and Phoenicurus phoenicurus) and only one species was a resident bird (S. melanocephala, Izhaki et al., 1990). The quantitative impact of these birds on seed removal varied between species with more than 50% consumed by S. atricapilla (Izhaki et al., 1990). As indicated for other Pistacia species (Jordano, 1989), frugivorous birds in Beit Jimal prefer fruits with viable seeds and ignore the pink-red fruits (Izhaki, 1986).

THE STUDY SITE

Observations were conducted in the western Jerzeel Valley in two plots: “Oranim”—on the Oranim campus of the University of Haifa, Israel (32°43’N, 35°07’E, 100 m altitude) and “Tivon”, 1 km west of Kiriya Tivon (1 km east of the first study plot). The annual mean temperature is 20 °C, and the mean relative humidity is 75%. The mean annual precipitation is 600 mm and there are 240 dew days per year. The site contained many fruit-bearing plants such as Pistacia palaestina, P. lentiscus, P. atlantica, Rhamnus alaternus, Laurus nobilis, Viburnum tinus, Lonicera etrusca, Rubia tenaxfolia, and Smilax aspera.

PROCEDURES

Maturation and disappearance of fruits were monitored in the “Oranim” plot on 13 marked trees by sampling them every 8–12 days from August to October 1993. Trees were chosen to represent a wide range of variation in fruit-crop size. The number of fruits (crop size) was estimated in early August by counting the number of fruits in 10–15 infructescences on each individual tree, calculating the mean number of fruit per infructescence and multiplying this mean by the number of infructescences per tree. In addition, tree height and dbh (diameter at breast height) were measured.

In early August, when only unripe red fruits were present and before fruit removal by frugivores began, 50–100 fruits were sampled from each marked tree and from ten additional trees from the “Tivon” plot to determine the extent of wasp larval infestation of the fruits, parthenocarpy, or abortion, and the development of viable seeds. Fruits were sliced open and examined for larval infestation. The fruit containing larvae, hereafter referred to as “infested fruits”, could later be externally
recognized on the tree by the presence of a small adult female emergence hole. These fruits remain red and resemble intact ones as observed in *P. terebinthus* (Traveset 1993b). No distinction was made between parthenocarpic and aborted fruits, and in all cases of partial development they were categorized as "undeveloped fruits". All fruits with fully developed seeds were categorized as "mature fruits". Only mature fruits change their color to bluish when ripe (for full description of these fruit types see fig. 1 in Traveset, 1993b). The mass of 50 mature fruits from each tree was measured.

On each sampling day the ripe and unripe fruits were counted on six selected branches on each tree to estimate the rate of fruit disappearance. Since fruits may drop rather than be removed by frugivores, five branches were protected from frugivores on each of the trees by covering them with net bags. However, as found before in this species (Izahki, 1986), as well as in *P. terebinthus* (Traveset, 1993a; Fuentes, 1995), unripe fruits remained on the tree for a long period and no abscission was observed until the end of the study. Therefore, all fruit disappearance in this study was due to removal by birds.

Two indices were calculated for dispersal success of a parent tree: (a) seed removal—the absolute number of viable seeds consumed by avian frugivores, and (b) dispersal efficiency (after Willson and Whelan, 1993)—the percent of total crop (ripe and unripe fruits) removed. This value is an estimate of the success in dispersing seed relative to the number of seeds produced by the parent plant. In effect, it is a benefit:cost ratio (see also Herrera, 1988, 1991; Jordano, 1991).

**STATISTICAL ANALYSIS**

Pearson’s correlation coefficient was calculated between (a) dispersal efficiency and the proportion of unripe fruits and (b) the proportions of infested fruits and undeveloped fruits. Multiple regression analysis of seed removal and dispersal efficiency with respect to crop size, tree height and diameter at breast height (dbh), fruit wet mass, proportion of infested fruits, and the proportion of unripe fruits was performed. Arcsine and logarithmic transformations were applied to proportions and number of fruits, respectively, before analyses.

**RESULTS AND DISCUSSION**

Trees were markedly different in their height (3–12 m height) and their crop size (1,586–180,480) with an average of 36,431 fruit per tree (Table 1). The latter value was twice that of the average of 19,382 fruits observed in ten trees in the Beit Jimal area (Izahki, 1986). The size of fruit crop of *P. palaestina* in Israel was 2–5 times that of *P. terebinthus* in Spain (Table 1). As expected, a positive correlation was detected between crop size and tree height ($r = 0.73$, $p = 0.0034$).

In the first observation on 15 August there were no bluish (ripe) fruits. The first ripe fruits were observed on 26 August with the proportion of bluish fruits increasing from 12% up to 25% on 4 October (Table 2). These percentages of ripe and unripe fruits in each date were an outcome of both fruit ripening and fruit removal, mainly of ripe fruits. Thus, red was the dominant fruit color in the infructescences during the entire study period. These results were similar to those obtained for *P. terebinthus* in southern Spain where only 17% of the fruits contained viable seeds and matured (Traveset, 1993a). However, the accumulated percentage of matured fruits of *P. palaestina* was >45 in this study and in

<table>
<thead>
<tr>
<th>Date</th>
<th>Ripe fruits (%)</th>
<th>Unripe fruits (%)</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>15 August</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>24 August</td>
<td>12</td>
<td>88</td>
<td>4.5</td>
</tr>
<tr>
<td>3 September</td>
<td>17</td>
<td>83</td>
<td>4.6</td>
</tr>
<tr>
<td>14 September</td>
<td>19</td>
<td>81</td>
<td>5.0</td>
</tr>
<tr>
<td>26 September</td>
<td>22</td>
<td>78</td>
<td>3.6</td>
</tr>
<tr>
<td>4 October</td>
<td>25</td>
<td>75</td>
<td>5.0</td>
</tr>
</tbody>
</table>

Table 1

Comparison of fruit production parameters [mean ± SE (n)] between *P. palaestina* in Israel and *P. terebinthus* in Spain

<table>
<thead>
<tr>
<th></th>
<th><em>P. palaestina</em></th>
<th><em>P. terebinthus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Crop size</td>
<td>(O) 3641 ± 13486 (13)</td>
<td>(B) 19382 ± 6085 (10)</td>
</tr>
<tr>
<td></td>
<td>4024 ± 525 (28)</td>
<td>8515 ± 170 (13)</td>
</tr>
<tr>
<td>Undeveloped fruits</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% parthenocarpic</td>
<td>18 ± 3 (28)</td>
<td>19 ± 3 (28)</td>
</tr>
<tr>
<td>% aborted fruits</td>
<td>70 ± 3 (28)</td>
<td>70 ± 3 (28)</td>
</tr>
<tr>
<td>Total (%)</td>
<td>(O) 30 ± 6 (13)</td>
<td>(B) 45.7 (10)</td>
</tr>
<tr>
<td></td>
<td>88</td>
<td></td>
</tr>
<tr>
<td>% wasp-infested fruits</td>
<td>(O) 16.5 ± 3.8 (13)</td>
<td>(B) 17.8 ± 2.6 (10)</td>
</tr>
<tr>
<td></td>
<td>9.0 ± 0.8 (129)</td>
<td>4.6 ± 1.2 (28)</td>
</tr>
<tr>
<td>Accumulated %</td>
<td>(O) 47 ± 4.4 (13)</td>
<td>(B) 63.5 ± 7.4 (10)</td>
</tr>
<tr>
<td>unripe fruits</td>
<td>&gt;90 (1994b)</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td></td>
<td>17 (1993a)</td>
</tr>
</tbody>
</table>

Table 2

Percentages of ripe and unripe fruits (mean ± SD) of *Pistacia palaestina* in northern Israel at each date

*Study plots: O-Oranim, T-Tivon (this study), B-J Beit Jimal (Izahki, 1986; Izahki et al., 1990). (b) Figures were taken from Traveset, 1993a,b and 1994a,b as indicated. (c) No distinction was made between parthenocarpic and aborted fruits in *P. palaestina*.*
the Judean Hill study (Table 1). The remaining proportion of fruits in Oranim (47%) comprised 30.5% undeveloped fruits (parthenocarpic and aborted fruits) and 16.5% infested fruits (wasp damaged). It seems that the proportion of parthenocarpic and aborted fruits was three times higher in P. terebinthus in Spain where 18% of the fruits were parthenocarpic and 70% were aborted (Table 1).

A negative correlation was detected between the percentage of wasp-infested fruits and the proportion of parthenocarpic and aborted fruits (Fig. 1). Traveset (1993b) showed such relationships between parthenocarpic fruits and wasp-damaged fruits in P. terebinthus. As no correlation was detected between wasp damage and crop size, it seems that wasp damage was not density dependent as reported in other studies of insect infestation of fruits (Courtney and Manzur, 1985; Jordano, 1987; Traveset, 1994).

Although the maximum distance between the studied trees at Oranim was less than 400 m, the variation in wasp damage was remarkable. The average proportion of damaged fruits caused by wasps was 16.5% ± 13.5% (coefficient of variation = 82%) of the seed crop but in 7 individuals the damage level was ≤10%, including one with no damage. In three individuals the damage was ≥30% with a maximum value of 45%. The variability in wasp damage was lower in Tivon where the coefficient of variation was 46%. The average damage reported here was much higher than the average <10% damage observed in P. terebinthus in several locations and studies in Spain (Table 1). The maximum value in Spain was 50% (Traveset 1993b) which was similar to the maximum found in P. palaestina (Table 1).

The maximal fruit removal rate was observed in the second half of August but frugivores continued to consume fruits until the beginning of October (Fig. 2). The average dispersal efficiency observed in this study was 38% ± 12.4% (range 21–65%) from the total number of fruits produced that were 72% of the ripe fruits. These figures were slightly lower than in a previous study in the Judean Hills (Izhaki, 1986) where 45% (100% of the ripe fruits) of P. palaestina fruits were removed by birds (Izhaki et al., 1990). In contrast to Pistacia terebinthus where the majority of the ripe fruits were consumed by bird seed predators (Traveset, 1994b), here all ripe fruits were removed by legitimate frugivores.

Three variables significantly affected seed removal, explaining 92% of its variation (Table 3). There was a positive correlation between seed removal, crop size, and tree height. A negative nonsignificant correlation was observed between seed removal and the proportion of infested fruits. Among all these factors affecting seed removal, crop size was the most important one. Crop size was also found to have the most consistent discernible variable affecting dispersal efficiency, in terms of number of fruits removed by frugivores, in many other fruit-bearing plants (e.g., Herrera, 1988; Jordano, 1989; Sargent, 1990).

The dispersal efficiency per individual plant was negatively correlated with the proportion of red (unripe) fruits in the crop of each individual along the study period (Fig. 3, r = −0.86, p = 0.0002, n = 13, arcsin squared-root transform data). Three factors may account for this observation. First, decreasing accessibility: unripe fruits and their supporting structure may present a physical barrier to frugivorous birds, preventing them from reaching the ripe fruits (Fuentes, 1995). Second, decreasing visibility: the massive red crop may mask the ripe crop from frugivorous birds (Fuentes, 1995). Third, frugivores consume only ripe fruits, so a large proportion of unripe crop would apparently end with low dispersal efficiency and vice versa. The multivari-

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**Fig. 1.** The correlation between the percentage of wasp-infested fruits and undeveloped fruits (including aborted and parthenocarpic fruits) of *Pistacia palaestina.*

**Fig. 2.** The percentage of *Pistacia palaestina* fruit crop (± s.d.) remaining on each date as a consequence of fruit removal by frugivorous birds.

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Table 3

Relationships between dispersal success (seed removal and dispersal efficiency) and morphological and fruit-related variables.
The relationships were determined by stepwise multiple regression

<table>
<thead>
<tr>
<th>Independent variables</th>
<th>Regression coefficient</th>
<th>Partial R²</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crop size</td>
<td>2233</td>
<td>0.52</td>
<td>0.010</td>
</tr>
<tr>
<td>Tree height</td>
<td>624</td>
<td>0.44</td>
<td>0.044</td>
</tr>
<tr>
<td>Tree dbh</td>
<td>29</td>
<td>0.04</td>
<td>0.025</td>
</tr>
<tr>
<td>Fruit wet mass</td>
<td>176</td>
<td>0.18</td>
<td>0.056</td>
</tr>
<tr>
<td>Proportion of infested fruits</td>
<td>-4987</td>
<td>0.06</td>
<td>0.19</td>
</tr>
<tr>
<td>Proportion of unripe fruits</td>
<td>-1459</td>
<td>0.02</td>
<td>0.68</td>
</tr>
</tbody>
</table>

Dispersal efficiency 0.08 0.89 4.63

Proportion of unripe fruits -0.588 0.74 0.018
Proportion of infested fruits -0.143 0.003 0.41
Fruit wet mass 0.003 0.11 0.41
Tree dbh -0.0003 0.08 0.55
Tree height 0.002 0.0002 0.87
Crop size 0.004 0.008 0.88

A regression analysis did not detect any other variable that significantly affect dispersal efficiency other than the proportion of unripe fruits (Table 3).

Although the preceding analyses are based on a limited sample, the results strongly suggest that *P. palaestina* in eastern Mediterranean habitats produces a larger fruit crop, faces lower seed predation by infesting wasps, and has a higher value of parthenocarpy and fruit abortion than *Pistacia terebinthus* in west Mediterranean habitats. Furthermore, fruit removal and dispersal efficiency of the former is much higher than the latter. However, the fate of the dispersed seeds in the deposited site depends upon several factors such as post-dispersal seed predation. As long as these data are not available, it is too early to compare the general reproductive success of these two congeneric species.

Acknowledgments

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Fig. 3. The correlation between dispersal efficiency of *Pistacia palaestina* and the percentage of unripe fruits.
Willson, M.F. and J.N. Thompson. 1982. Phenology and ecology of color in bird-dispersed fruits, or why some fruits are red when they are "green". Canadian Journal of Biology 60: 701-713.