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The effect of unripe fruits on ripe fruit removal by birds in *Pistacia terebinthus*: flag or handicap?

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Abstract The shrub *Pistacia terebinthus* produces crowded infructescences with up to several hundred fruits, which are bright red when unripe and turn green when ripe. Most fruits contain an empty seed and never reach maturity. More ripe fruits were removed by birds from experimental bicolored fruit displays (consisting of infructescences with ten ripe fruits and stripped of unripe fruits, paired with infructescences with only unripe fruits) than from monocolored ones (single infructescences with ten ripe fruits and stripped of unripe fruits). Thus, the presence of unripe fruits seems to increase the conspicuousness or attractiveness of fruit displays to fruit-eating birds. A second experiment compared ripe fruit removal from experimental infructescences having only ripe fruits, with that from control infructescences containing both ripe fruits and natural numbers of unripe fruits, all on *P. terebinthus* plants. Unlike the first experiment, each bicolored display in this case consisted of a single infructescence with both unripe and ripe fruits. A higher proportion of ripe fruits was removed by birds from infructescences free of unripe fruits. This result suggests that the presence of unripe fruits reduces the accessibility of ripe fruits for fruit-eating birds. This is further supported by field observations of bird foraging behavior.

Key words Bicolored display · Bird · Fleshy fruit
Seed dispersal · Surplus fruits

Introduction

The brightly colored unripe fruits of some plant species may act as “flags” that advertise the presence of ripe fleshy fruits to avian seed dispersers. If such a bicolored display increases seed dispersal success of plants, asynchronous ripening of fruits and conspicuous coloration

of unripe fruits may be favored (Willson and Thompson 1982; Willson and Whelan 1990a). Such a bicolored fruit display apparently increases the probability that fruit-eating birds will find an infructescence of *Prunus serotina* and feed on its fruits (Morden-Moore and Willson 1982; Willson and Melampy 1983; Janson 1987).

I suggest, however, that in some cases the presence of unripe fruits may render at least some of the ripe fruits inaccessible to birds. This may result from two nonmutually exclusive mechanisms. First, unripe fruits, together with their supporting structures, may present a physical barrier to foraging birds. Second, large numbers of unripe fruits may decrease the visibility or even completely hide ripe fruits from foraging birds. Thus, the presence of unripe fruits may have two opposing effects on ripe fruit removal by birds: (1) increasing the conspicuousness of the fruit display, but at the same time (2) reducing the number of fruits that can be taken by birds finding the fruit display, thus slowing the rate of removal. Slower fruit removal rates by seed dispersers can result in increased fruit losses to predators and pathogens and/or in more even dispersal of seeds in time and space, which may influence seed survival.

In this study of *Pistacia terebinthus* I evaluate the effect of the presence of unripe fruits on the rate of ripe fruit removal by frugivorous birds. In particular, I ask whether they act as a flag that attracts avian consumers, and/or as a handicap that hinders their foraging on ripe fruits.

Material and methods

Natural history of the species

P. terebinthus is a shrub or small tree that produces crowded infructescences containing up to a few hundred full-sized fruits. Unripe fruits are bright red and strikingly visible, at least to the human eye. Because of parthenocarpy, embryo abortion or insect attack, most contain inviable seeds. However, abscission does not occur, and empty fruits remain on the plant even after all ripe fruits have been removed or have fallen (Traveset 1993a; M. Fuentes, unpublished data). Empty fruits and filled unripe fruits are

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externally indistinguishable. Traveset (1993b) found that the presence of parthenocarpic fruits in *P. terebinthus* reduces the proportion of viable seed attacked by insect predators that oviposit before fruits begin ripening.

The fruits of *P. terebinthus* grow in panicles that are located near the ends of branches. Each branch bears one or more panicles growing so close together they are usually intermingled. I call a set of such associated panicles an "infructescence." Infructescences are typically globular, dense tangles of peduncles and fruits.

Throughout this study, "unripe" fruits refers to both fruits containing inviable seeds that will never ripen and fruits with filled seeds that have not yet ripened. Unripe fruits are bright pinkish-red or pinkish-red with yellow, and fully ripe ones are green or bluish-green. Avian seed dispersers strongly prefer green fruits and eat an insignificant proportion of red fruits (Traveset 1993a; M. Fuentes, personal observation).

In southeastern Spanish populations of *P. terebinthus* only about 17% of final-sized fruits contained viable seeds and matured (Traveset 1993a). The percentage was also very low in my study area (M. Fuentes, personal observation). Fruits ripen asynchronously over about a 1 month period. They are readily eaten by frugivorous birds (Traveset 1993a; M. Fuentes, personal observation), so only a few ripe fruits can be found at any given time in an infructescence. A detailed account of other aspects of the reproductive biology of *P. terebinthus* can be found in Traveset (1993a).

Methods

This study was conducted at several sites around the Penarrubia Dam, Ourense province, northwestern Spain. In this region *P. terebinthus* grows in several habitat types, such as rocky cliffs, stony places, and evergreen oak (*Quercus rotundifolia*) shrublands.

I counted the number of fruits in 76 infructescences on 16 plants on each of five dates during August and early September 1992 in one of my study plots (El Estrecho). This covered the whole period of ripe fruit availability. The mean number of final-sized fruits per infructescence was 156 (range 24–600). Thirty four infructescences (45%) had ripe fruits present on at least one of the counts. For infructescences with at least 1 ripened fruit, the mean maximum number of ripe fruits per infructescence was 10 and the maximum was 36. Counts were repeated in 1993, when the mean number of fruits per infructescence was 112 (range 6–555), and the mean diameter of the infructescences was 20 cm ($n=146$ infructescences of 40 plants). In four fruit counts during late August and September 1993 that encompassed the entire period of ripe fruit availability, ripe fruits were found on only 11 of the 146 infructescences sampled. The maximum number ever found in a given infructescence was five.

I conducted two separate experiments. The first was designed to test the flag effect by monitoring fruit removal from infructescences containing only ripe fruits in two kinds of displays. Monocolored displays consisted of single infructescences bearing only ripe fruits; bicolored displays consisted of equivalent infructescences bearing only ripe fruits but paired with infructescences containing only unripe fruits. Thirty six infructescences were removed from plants and placed on the vertical surfaces of rock outcrops in a steep, open habitat, where past grazing had limited the presence of *P. terebinthus* to pre-reproductive individuals. This is not an unnatural situation since infructescences of *P. terebinthus* growing in rocky habitats are often positioned close to rock surfaces. All fruits except for 10 ripe ones were removed from each of 24 infructescences. Twelve of these infructescences were placed singly, and 12 paired with another infructescence from which I had removed all ripening and ripe fruits. The number of unripe fruits remaining was not counted, but ranged from several dozen to a few hundred. The paired infructescences were less than 10 cm apart, but not touching each other. This set-up allows the potential attraction of the bicolored "flag" display, yet avoids the possibility of unripe fruits hindering access to ripe fruits. Displays were usually >10 m apart, and out of sight of each other. Infructescences

were connected to water bags and their fruits apparently remained intact for several days; without a water supply fruits deteriorate in a few hours. I made every effort to hide the water bags and tubes, but it was unavoidable that parts of them were visible. After 2 days I counted the number of ripe fruits remaining on the infructescences.

The second experiment was designed to test the handicap effect. In this case I compared ripe fruit removal from natural pairs of infructescences that differed only in the presence or absence of unripe fruits. Since infructescences were not removed from their parent plants they were both subject to the same potential flag effect at the level of the entire tree. I manipulated 2 infructescences on each of 17 plants. On one infructescence per tree I removed all unripe fruits; on the other infructescence I left all the unripe fruits. I then adjusted the number of ripe fruits so that an equal number (between 4 and 22) remained on the 2 infructescences on a given tree. I did not count the number of unripe fruits remaining on the second category of infructescences, but their number ranged from several dozen to a few hundred. I counted the number of ripe fruits remaining on the infructescences once within 2 days of the manipulation.

All experiments were conducted between 22 August and 10 September 1993. In each experiment I removed all fruits that were beginning to ripen, precluding the possibility that some unripe fruits ripened before the experiment ended. No evidence of damage by greenfinches (*Carduelis chloris*) or rodents was found on the infructescences used for the experiments, suggesting removal was by seed dispersers.

In addition to the experiments, I made direct observations of fruit-eating by birds in August and September 1992, in order to gather information on both the identity of consumers of *P. terebinthus* fruits and their foraging behavior. I made observations on several plants in the El Estrecho plot, recording the number of fruits eaten by each bird visiting a plant, as well as their behavior while searching for and feeding on fruits.

Results and discussion

A higher proportion of ripe fruits was removed from infructescences placed close to unripe displays than from solitary infructescences (Fig. 1, flag effect; Wilcoxon-Mann-Whitney test $W_x=121$, one-tailed $P=0.044$). Three monocolored displays, compared to only one bicolored display, had no fruit removal during the 2 days of exposure. Thus, a weak flag effect was supported by this experiment. Previous studies have also found flag effects caused by unripe fruits, ancillary structures and artificial leaves, although not as consistently as expected (Morden-Moore and Willson 1982; Stiles 1982; Willson and Melampy 1983; Willson and Hoppes 1986; Facelli 1993). In the case of the present study the flag effect could be caused by the bright coloration of unripe fruits or by the increased "total crop size" of the bicolored displays. Evidence from previous studies indicates that larger fruit displays do not usually result in a higher proportion of fruits being removed by birds (see Carr 1992).

In the second experiment, a higher proportion of ripe fruits was removed from infructescences stripped of unripe fruits than from paired control infructescences containing both ripe and unripe fruits (Fig. 1, handicap effect; Wilcoxon signed ranks test $T=0$, one-tailed $P<0.001$). All fruits were removed within 2 days from seven monocolored displays, but from only two bicolored ones. Thus, the presence of unripe fruits appears to

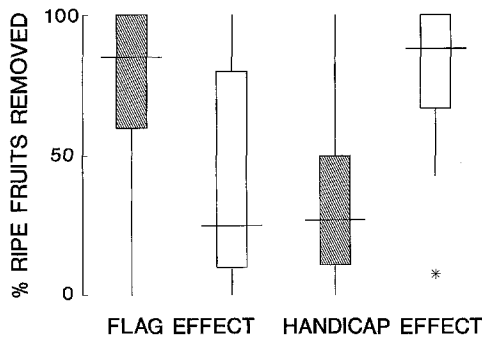


Fig. 1. Box-and-whiskers plots of the percentage of ripe fruits removed from monocolored and bicolored displays. The two plots on the left test for the flag effect, and the two plots on the right test for the handicap effect. Horizontal lines are the medians, boxes encompass the first to third quartiles, and vertical lines show the 95% confidence intervals. Shaded boxes correspond to bicolored fruit displays and white boxes to only-ripe fruit displays. In the case of the monocolored displays used in the handicap experiment, an outlier is shown with an asterisk. In the case of the handicap effect, note that experimental and control infructescences were paired, not independent; the distributions are graphed separately for ease of comparison

decrease the removal rate of ripe fruits by hindering foraging by birds by decreasing either visibility and/or accessibility of ripe fruits. A handicap effect could also be considered as a possible explanation for the finding that fewer fruits were removed from bicolored fruit displays of *Prunus serotina* than from monocolored displays (among those displays found by birds; Janson 1987) in the study by Willson and Melampy (1983). Previous studies have experimentally documented the importance of fruit accessibility for foraging frugivorous birds (Denslow and Moermond 1982; Moermond and Denslow 1983; Levey et al. 1984).

During observations of *Pistacia terebinthus* plants I recorded 116 bird visits in which at least one fruit was eaten. The total number of fruits consumed was 280. The most frequent avian consumers were *Phoenicurus ochruros* (31% of visits), *Sylvia cantillans* (21%), *Carduelis chloris* (17%), *Phoenicurus phoenicurus* (13%) and *Sylvia atricapilla* (11%). The set of dispersers was similar to that found by Traveset (1993a) in southeastern Spain. Among seed dispersers, the mean number of fruits eaten per visit was 1.1 (range 1.0–1.2).

My observations support the conclusion that the presence of unripe fruits hampered bird foraging on ripe fruits. First, the difficulties faced by birds when trying to find and reach ripe fruits were quite evident. The typical foraging sequence of *Phoenicurus* spp. consisted of: (1) hovering at a distance of about 10 cm in front of an infructescence, apparently searching for ripe fruits, (2) momentarily perching on the ground or on a nearby branch, and (3) hovering again to pick a fruit. Steps 1 and 2 were often repeated several times, apparently until an accessible ripe fruit was located. Additionally, step 3 often ended in failure. *Sylvia* spp., which foraged while perched on the infructescences or on nearby branches, also often

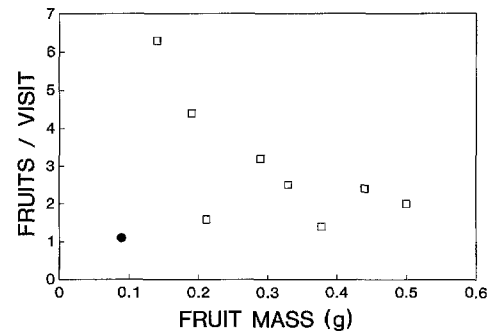


Fig. 2. Mean number of fruits eaten by *Sylvia atricapilla* per visit (for visits in which at least one fruit was eaten) to several plant species, and the relationship to the fresh mass of fruits (g). The circle corresponds to *Pistacia terebinthus* (present study). The data for the remaining species were taken from Herrera and Jordano (1981), Snow and Snow (1988) and J. Guitián (personal communication, for *Cornus sanguinea*)

failed to reach any of the ripe fruits present in the infructescences. Traveset (1993a) observed *Coccothraustes coccothraustes* (a seed predator) “cutting infructescences (panicles) with red fruits and rejecting them to reach the green ones.” Second, the number of fruits eaten per visit to *P. terebinthus* plants was much lower than that expected given the size of fruits (0.089 g, based on 30 fruits collected in the area) and birds (10–17 g) involved (Snow and Snow 1988; Jordano 1992; see Fig. 2 for *Sylvia atricapilla*). Low ripe fruit availability on the plants cannot fully account for this finding because the plants selected for the observations had as many as several dozen ripe fruits. I suggest that the presence of unripe fruits resulted in many ripe fruits being unavailable to birds.

In summary, the presence of unripe fruits apparently attracts fruit-eating birds to infructescences because of increased conspicuousness, but negatively affects the accessibility of ripe fruits to the birds attracted to these infructescences. The first effect increases the removal rate of ripe fruits while the second reduces it. It is possible that the flag effect in typical plants of *P. terebinthus*, that bear as many as several dozen infructescences, is stronger than in the displays used in the present study. In any case, it has been found that plants with more empty fruits do not experience higher ripe fruit removal rates (Traveset 1993a, 1993b; see also Jordano 1989 for *Pistacia lentiscus*).

At least three characteristics of seed dispersal success of parent plants may be affected by the results reported here: (1) the number of ripe fruits lost to seed predators and pathogens, (2) the timing of seed dispersal, and (3) the spatial pattern of seed dispersal. Evidence thus far suggests virtually all ripe fruits are eaten by birds (Traveset 1993a; M. Fuentes, personal observation). Traveset (1993a) found no evidence of insect attack on already ripened fruits, suggesting a faster removal rate would not result in reduced levels of insect damage. However, faster fruit removal by seed dispersers may reduce the loss of fruits to granivorous birds. As for the second characteristic, fruit removal rate (together with ripening pheno-

logy) influences the timing of seed dispersal, which in turn may affect the fate of seeds on the ground. For example, late dispersed seeds may experience different predation rates by ants or rodents than early dispersed ones (Willson and Whelan 1990b; Whelan et al. 1991). Given the very short seed dispersal period of *P. terebinthus*, it is unlikely that the variation in removal rates found here would have a significant effect on the fate of dispersed seeds. Finally, it may be advantageous for the parent plant to have dispersers ingesting small amounts of fruits per visit since this may lead to dispersal to a greater diversity of seed desposition sites and less clumping than they would if more seeds were consumed at one time.

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