The effect of deceptive fruits on predispersal seed predation by birds in *Pistacia lentiscus*

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Abstract

Deceptive fruits (fruits containing empty seeds and seedless fruits) in the dioecious shrub *Pistacia lentiscus* L. (Anacardiaceae) remain attached to the plant throughout the dispersal season. This study addresses the hypothesis that deceptive fruits may contribute to parental fitness by reducing predispersal seed predation by granivorous birds because these fruits represent handling costs to predators and they prefer to forage selectively on shrubs with filled fruits. This study was run in two populations of *P. lentiscus* and finds that deceptive fruits reduce seed predation by granivorous birds but only in the population that presented higher *P. lentiscus* female density, and a higher variability in the percentage of deceptive fruits among *P. lentiscus* females. Under this scenario, the benefits of flying to another female might be higher than those of remaining in the same female searching filled seeds. By contrast, the costs of flying to other females, when they are scarce and have a similar percentage of deceptive fruits may be higher than the benefits.

Introduction

Seedless fruits and fruits with empty seeds are the results of ontogenetic processes that lead to parthenocarpy and abortion (Gillaspy et al. 1993). These fruits that are maintained by the plant are puzzling because they would appear not to contribute to parental fitness. Various hypotheses have been proposed to explain their existence (Janzen 1971a, 1971b; Willson and Burley 1983; Zangerl et al. 1991; Traveset 1993; Fuentes and Schupp 1998; Verdú and García-Fayos 1998a). Many of these studies have documented different mechanisms in which these fruits reduce seed predation, by deceiving the insects. Most of these mechanisms are related to the inability of insect predators to discriminate between deceptive fruits and those containing filled seeds (but see Zangerl et al. (1991) for a chemical mechanism). However, it is well known that seed predation by vertebrates, like granivorous birds, may represent high losses of filled seeds (Willson 1983; Verdú and García-Fayos 1995). Fuentes and Schupp (1998) have recently considered the role of deceptive fruits on vertebrate seed predators (*Parus inornatus*) choice of *Juniperus osteosperma* plants. They documented that the trees suffering high levels of *P. inornatus* seed predation also had a higher proportion of filled seeds. It suggests that predators prefer to forage selectively on trees with filled fruits to reduce the handling costs associated with deceptive fruits.

Verdú and García-Fayos (1998a) found that the presence of aborted seeds in *Pistacia lentiscus* shrubs, reduced seed predation rates by chalcidoid wasps in the same way that parthenocarpic fruits did in *Pistacia terebinthus* (Traveset 1993). These benefits would only be restricted to the time when ovules have not enlarged and therefore wasps cannot discriminate between filled and deceptive fruits. However, deceptive fruits (both parthenocarpic fruits and aborted seeds) remain attached to the plant during the fruiting season. Deceptive fruits in *P. lentiscus* could also reduce seed predation by granivorous birds. The aim of this study was to test if deceptive fruits can reduce predispersal seed predation by birds.

Study sites

Estimations of both predispersal seed predation by granivorous birds and the frequency of deceptive fruits in *P. lentiscus* females were made in two populations during the fruiting season 1992–1993. These populations are Mediterranean sclerophyllous shrublands, located in Valencia, eastern Spain (Pujol and Porta Coeli), that differ in female density of *P. lentiscus* individuals (Verdú and García-Fayos 1998b). Pujol has the higher female density with 121 ♀/10 ha, whereas PortaCoeli has a density of 90 ♀/10 ha.

Study species

Pistacia lentiscus L. is a common dioecious shrub in Mediterranean sclerophyllous shrublands. It is evergreen and wind pollinated. Females produce many one-seeded drupes (see Jordano (1988, 1990) for more details and Grundwag (1976) for embryology and fruit development). The colour of the fruits is associated with seed viability because black fruits usually contain filled seeds whereas white and red fruits contain no seeds or empty seeds. In *P.lentiscus* populations from southern Spain, Jordano (1988, 1989) reported that only 5.8% of the black fruits contained empty seeds.

Frugivorous birds disperse seeds from September to March (Herrera 1984; Jordano 1989; Verdú and García-Fayos 1994, 1995). Ants can act as secondary dispersers (Aronne and Wilcock 1994). Predispersal seed predation is mainly performed by chalcidoid wasps (*Megastigmus pistaciae*) and granivorous birds (mainly *Carduelis chloris*) (Jordano 1990; Verdú and García-Fayos 1998a). Jordano (1990) observed that *C. chloris* may handle 5 fruits of *P. lentiscus* per minute but only 3 seeds are ingested because deceptive fruits are discarded. Post dispersal seed predation is performed by rodents and granivorous birds (Verdú and García-Fayos 1996a). A transient seed bank is formed and rapid germination within the year occurs (García-Fayos and Verdú 1998). Seedling recruitment is associated with the presence of perches (Verdú and García-Fayos 1996b).

Methods

At the start of the fruiting season (September, 1992), we counted all the fruits from several infrutescences in 22 females selected randomly from 2 populations (13 females in Porta Coeli, and 9 females in Pujol). These infrutescences (controlled infrutescences hereafter) contained on average 15.2 ± 4.4% of the total crop of the plant in both populations (there were no statistical differences between populations). One plastic tray per shrub was placed under controlled infrutescences to collect the seed coats thrown under the branch by predators. Each tray measured approx. 0.2 m^2 and sampled around 5% of the canopy projection. Trays were covered with a wire mesh to avoid animals removing seed coats. Seed coats were collected and counted weekly throughout the dispersal season from September 1992 until the controlled infrutescences were depleted (April 1993). Seed coats were easy to count because they were presented as two empty halves inside the tray. The percentage of eaten seeds was estimated as the ratio "eaten seeds/ initial number of fruits in the infrutescence". This ratio may underestimate the number of seeds eaten if some seed coats fall outside the tray. While this limitation is relevant to absolute predation rates, we expect it to apply equaly to all studied individuals. Therefore, we consider it irrelevant to our study.

The percentage of deceptive fruits was also estimated at the start of the dispersal season (September 1992) by checking seed presence and viability in at least 50 fruits per female (see Jordano (1988, 1989) for an explanation of the morphology of deceptive fruits).

Results

Fruit colour was not a very good clue for seed viability, due to the fact that the percentage of deceptive fruits that were black was 37.8% for the Pujol (n = 82) population, and 44.2% for the Porta Coeli (n = 104) population.

Seed predation rate was significant and inversely correlated with the percentage of deceptive fruits only in the Pujol population, as shown in Figure 1. In addition to this, many female shrubs in the Porta Coeli population presented a similar percentage of deceptive fruits (11 out of the 13 study shrubs had between 90% to 100% of deceptive fruits). In contrast, female shrubs in Pujol ranged continuously from 72% to 98%.

The significant relationship between seed predation and deceptive fruits is negative, indicating that a higher percentage of deceptive fruits reduces the per-
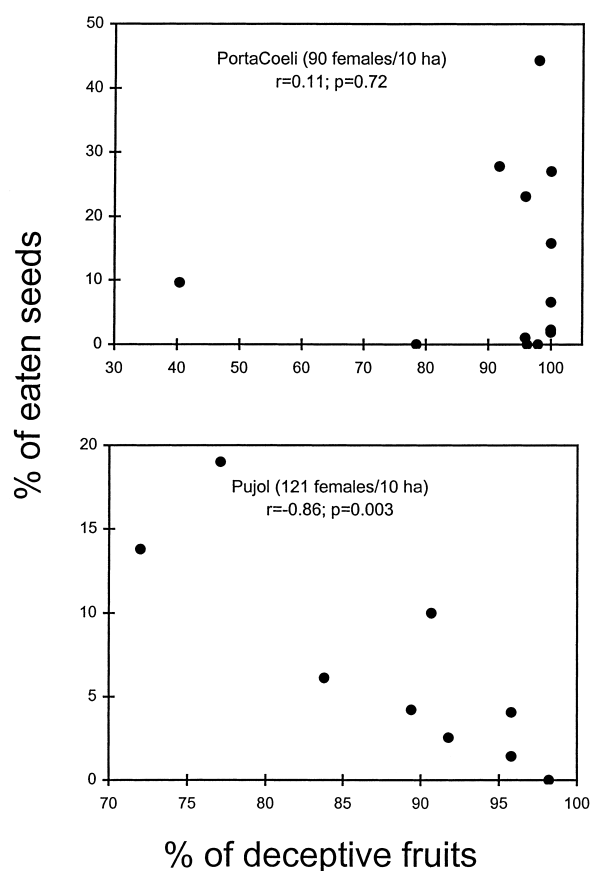
Figure 1. Relationship between seed predation by birds and deceptive fruits, expressed as the percentage of total fruit crop per tree, in two populations.

centages of eaten seeds by birds. Neither the percentage of eaten seeds (r = −0.36; p = 0.34) nor the percentage of deceptive fruits (r = 0.12; p = 0.76) correlate to the crop size (data not shown).

Discussion

The results of this study show that deceptive fruits (parthenocarpic fruits and fruits containing aborted seeds) in *Pistacia lentiscus* reduce seed predation by granivorous birds in one of the two study populations. Verdú and García-Fayos (1998a) found a similar negative relationship between the percentage of seed predation by wasps and that of aborted seeds. Janzen (1971a, 1971b) stated that two conditions were necessary to consider the presence of deceptive fruits to be an adaptation to reduce predispersal seed predation. The first is that empty seeds must develop early in the ontogenesis of the fruit to minimize costs to the parent plant. The second is that the number of eaten seeds must be independent of the crop size. In this study, both conditions were met. Based on colour and consistency of the tissues within the seeds (as described by Jordano (1989)), at least 70% of aborted seeds were done so at an early stage in fruit development, and parthenocarpy is produced from the first development stage of the fruit, satisfying the first condition. Our findings of no relationship between crop size and the percentage of eaten seeds satisfy the second condition. For these reasons, the adaptive (or pre-adaptive) value of deceptive fruits in reducing seed predation is not only related to the first wasp generation, but also to bird seed predation that acts throughout the whole fruiting period. With this in mind, it is easier to understand why deceptive fruits remain attached to the plant so long.

Fuentes and Schupp (1998) documented that deceptive fruits of *Juniperus osteosperma* reduce seed predation by *Parus inornatus* because there is a cost in handling fruits containing empty seeds, and therefore birds prefer to forage selectively on trees with filled fruits. Handling costs for granivorous birds (*Carduelis chloris*) foraging on *P. lentiscus* fruits have been studied by Jordano (1990), who describe the bill-weighing behavior displayed by these birds to detect viable seeds and reject deceptive fruits. Fruit colour is a good clue for the birds to minimize handling costs because it is associated with the seed viability. However, the association is not perfect because many deceptive fruits are black (37.8% and 44.2% in populations from this study), and therefore handling costs remain despite this clue. Therefore, irrespective of fruit colour, high percentages of deceptive fruits in the study plants increase handling costs. Consequently, birds may prefer to fly to another shrub carrying higher percentages of filled seeds. Nevertheless, the costs of flying to another shrub may be higher than benefits if 1) the density of female shrubs in the population is low, and 2) many female shrubs in the population present a similar percentage of deceptive fruits. These could be the reasons why a negative relationship between the percentages of deceptive fruits and eaten seeds was not found in both populations of this study. Only in the population with a high density of females with differing percentages of deceptive fruits, did deceptive fruits appear to reduce seed predation. Other site-specific attributes, not included in this study, may also be associated to predispersal seed predation, and therefore more replicates (populations) should be studied to ensure that both high density of

females and high frequency of deceptive fruits reduce seed predation.

In summary, deceptive fruits may reduce seed predation by birds in *P. lentiscus* under particular conditions that increase fruit handling costs to seed predators. These conditions include: 1) shrubs must differ in the percentage of deceptive fruits 2) costs of moving among fruiting individuals must be low relative to the cost of increased handling time. These costs may include the metabolic costs of actual movement, as well as the increased risk of predation on the seed predator itself (Brown 1999).

Acknowledgements

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