

Bird rejection of unhealthy fruits reinforces the mutualism between juniper and its avian dispersers

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We investigated fruit damage by insects as well as fruit abortion in relation to the mutualism between *Juniperus communis*, a fleshy-fruited plant dominant in the high mountains of southeastern Spain, and its bird disperser assemblage. For two years, we performed field experiments to analyse fruit selection by birds, offering birds different types of anomalous fruits (unripe, aborted, pulp-sucker infested and seed-predator attacked) and comparing the removal rate to that of ripe, healthy, control fruits. In addition, we studied the proportion of fruits attacked by the seed predator in samples of fruits which, after manipulation and rejection by birds, we found lying underneath plants. We compared these data to values in samples of fruits which we took directly from plants. Finally, over four years, the abundance of predispersal-depredated seeds in the seed rain dispersed by birds was compared with the abundance in seeds taken directly from plants. Fruit-choice experiments showed that unripe, aborted and fruits attacked by pest insects (both pulp sucker and seed predator) were strongly counterselected by these frugivorous birds. The proportion of fruits attacked by seed-predator in the sample of fruits manipulated and rejected was significantly higher than in the fruits taken from plants. For all study years, the proportion of depredated seeds was significantly lower in the sample of seeds dispersed by birds than in the sample of seeds taken from plants. Bird response to pests was not categorically to accept or reject fruit, but rather was influenced by pest density. Birds showed two different levels of fruit selection, depending on the type of fruit: visual discrimination, against fruits that are unripe, aborted and infested by the pulp sucker; and within-beak discrimination, against fruits attacked by the seed predator. In the study, both pests either died or left the fruit when ripe, and therefore frugivorous birds did not interfere directly with frugivorous insects. On the contrary, insects did interfere indirectly with birds, promoting the rejection of pest-attacked fruits by birds. Bird dispersers overcame the predispersal interference of pest fruit damage and fruit abortion and increased the proportion of healthy seeds in the seed rain. This fact, together with the great quantity of seeds dispersed by birds, reinforces the importance of birds as plant mutualists.

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Fruits are more nutritious for animals than are many other plant organs (Howe and Westley 1988). Consequently, ripe fruits represent an attractive reward not only to mutualistic animals which disperse the seeds contained in the fruit, but also to small parasitic herbivores such as seed predators and pulp eaters (Janzen 1971, Herrera 1982). Fleshy-fruited plants, vertebrate dispersers and

fruit pests make a complex ecological triad in which each component interacts directly and/or indirectly with the other two (Herrera 1984, Jordano 1987, Buchholz and Levey 1990). As a result of the plant-pest-disperser triad, plant fitness is determined by the balance between two opposing direct interactions with the plant: pest-plant antagonism and disperser-plant mutualism.

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The outcome of the interaction between pests and frugivorous dispersers, and their respective relative effects on plant reproductive success will be strongly influenced by the dispersers' reaction to pest-damaged fruits (Manzur and Courtney 1984). Within their natural habitats, frugivorous vertebrates can show a fruit-selection behaviour towards fruit size and shape, chemical composition and accessibility (Jordano 1992, Whelan and Willson 1994). Vertebrate frugivores usually respond to pest infestation by rejecting such fruits, depending on the kind of pest attacking the fruits and/or the alteration in fruit traits induced by pest attack (Sallabanks and Courtney 1992; but see Redford et al. 1984, Valburg 1992a, b). As a consequence, fruit pests directly affect the plant by reducing the number of healthy seeds produced by the plant, but also indirectly, reducing fruit attractiveness to frugivorous dispersers (Janzen 1977, Jordano 1987, Borowicz 1988, Dixon et al. 1997).

Despite the increase in the number of works published on the plant-pest-disperser system, many unanswered questions remain (Sallabanks and Courtney 1992). Most studies have analysed the selective behaviour of avian dispersers in relation to the pest-attacked fruits under aviary conditions (Borowicz 1988, Buchholz and Levey 1990, Valburg 1992b, Cipollini and Stiles 1993, Traveset et al. 1995, Dixon et al. 1997, Hubbard and McPherson 1997). However, few of these studies have tested the correspondence between the experimental results and the outcome of pest-disperser interaction in the field (but see Valburg 1992a, Traveset et al. 1995). Another main research topic has been the overall analysis of the interactive triad between dispersers, pests and plants (Herrera 1984, 1989, Manzur and Courtney 1984, Burger 1987, Jordano 1987, Krischik et al. 1989, Christensen and Whitham 1991, Traveset 1992, 1993). Most of these works have used observational data to relate the abundance of both dispersers and pests, as well as the co-occurrence of pests and dispersers, to their interaction with the plant. However, experiments designed to test the patterns observed in the field are lacking (but see Christensen and Whitham 1991, Traveset 1992). On the other hand, a main drawback of studies on plant-pest-disperser system is that the consequences for plant fitness have been analysed at the level of fruit removal by dispersers (Courtney and Manzur 1985, Burger 1987, Jordano 1987, Valburg 1992a, Traveset 1993, Traveset et al. 1995). However, it would be more informative to analyse whether the consequences of the interaction are translated to the stage of seed rain, the bridge between plant predispersal ecology and population recruitment (Jordano and Herrera 1995).

The main goal of the present work is to characterize the effects that pest damage on fruits and fruit abortion have over the mutualism between fleshy-fruited plants and vertebrate dispersers. Using both observational and

experimental approaches, we have studied the system composed of juniper *Juniperus communis* L. (Cupressaceae), a dominant shrub in the high mountains of southeastern Spain, its full assemblage of bird dispersers and its main fruit pest insects – pulp suckers and predispersal seed predators. We determined whether the consequences of direct and indirect interactions between pests and birds are translated to seed rain, addressing the following questions: 1. Do bird dispersers select fruits on the basis of fruit abortion and pest damage? 2. Does the selective behaviour of birds depend on the kind of fruit pest and/or the pest-infestation level? 3. Is there any potential effect, direct or indirect, of dispersers on pest populations and vice versa? 4. What are the consequences for plant fitness due to the pest impact on mutualistic interaction between plants and dispersers?

Natural history of the system

J. communis is one of the gymnosperms with the widest distribution area in the Holarctic, with a continuous range in boreal and northern Europe but becoming isolated southwards to scattered mountain areas around the Mediterranean Basin (Polunin and Walters 1985). In the Mediterranean high mountains, such as the Sierra Nevada (SE Spain), juniper inhabits altitudes from 1600 to 2500 m a.s.l., being the main woody species above the treeline and producing the typical high-mountain juniper shrublands (Molero et al. 1992). Apart from the occasional *Berberis vulgaris*, *J. communis* is the only fleshy-fruited species in the shrubland. The study site is located at 2300 m a.s.l., in the area called Campos de Otero, where juniper cover exceeds 30% (García et al. 1996). Usually, the area remains under snow from early December to the end of March.

J. communis is dioecious, the female individuals bearing axillary initial cones each year that take three years to develop fleshy galbulae (fruits hereafter), containing 1–3 seeds per fruit. Three phases can be distinguished in the development from the initial cone to the ripe fruit (Roques et al. 1984): 1) pollination and delayed fertilization of the cone, during the first year; 2) fruit-growth phase, during the second year, producing a berry-like fruit with green colour, reaching the final size and developing seeds; and 3) fruit ripening, during the third year, the fruit colour changing in September to blue-grey. Cones are produced annually, and therefore it is possible to find initial cones and fruits of two different cohorts simultaneously in the same plant. During the summer of the fruit-growth phase, fruits may suffer abortion. The mean percentage of aborted fruits per plant is 56.01 (± 2.57 se, range = 5.0–91.0, $n = 75$ plants, García 1997). Aborted fruits, smaller and drier than healthy fruits, become grey-coloured and

shrivelled, and remain on the plant for a long period. All the seeds within aborted fruits are unviable.

In the Sierra Nevada, the fruits of *J. communis* are attacked by two main species of insects: a seed-predator chalcid, *Megastigmus bipunctatus* Swederus (Hymenoptera, Torymidae; *Megastigmus* hereafter), and a sessile sucking scale, *Carulaspis juniperi* Bouché (Homoptera, Diaspididae; *Carulaspis* hereafter). Ripe fruits may show *Megastigmus* exit holes, the white scales covering *Carulaspis* carcasses, and the round traces of fallen scales on the fruit surface. In addition, both fruits heavily infested by *Carulaspis* as well as those attacked by *Megastigmus* show a lower proportion of viable seeds than do unattacked fruits (García 1998).

Megastigmus adults emerge from ripening fruits in early summer, mate, and females oviposit in fruits at the beginning of fruit-phase 2. The larva develops within the seed and emerges as an adult the next summer, leaving the fruit by an exit hole (Vikberg 1966, Roques 1983). There is no evidence for prolonged diapause of *M. bipunctatus* larvae within *J. communis* seeds (Roques 1989, García 1998). The percentage of fruits attacked by *Megastigmus* per plant ranged from 1.0 to 83.0% (mean \pm se = 33.6 ± 2.3 , $n = 75$ plants), and at least 20% of the plants showed more than 50% of their fruit crop damaged by this seed predator. *Megastigmus* abundance varies significantly from year to year (García 1997).

Carulaspis infests fruits by attaching to the surface and covering itself with a waxy white scale. The mated females lay eggs in fruits at the beginning of fruit ripening, in May and June, and these hatch into first-instar crawlers which settle into the fruits at the beginning of fruit-phase 2. Female crawlers become sessile adults which feed on the surface of fruits. The mated female scale overwinter, start laying the next spring, and die in the summer, when the fruits are in phase 3 (Kosztarab and Kozar 1989). The mean percentage of fruits attacked by *Carulaspis* per plant is 54.2 (± 3.7 se, range = 0–85.7, $n = 29$ plants) but only 3.5% of the plants showed more than 50% of their fruits heavily attacked by *Carulaspis* (García 1997).

In the high mountains of the Sierra Nevada, ripe fruits are consumed by two species of frugivorous birds: ring ouzel (*Turdus torquatus*) and mistle thrush (*T. viscivorus*), which act as legitimate seed dispersers (Zamora 1990a, Jordano 1993). *T. viscivorus* is a sedentary species in the Sierra Nevada which appears in the juniper shrublands at the end of summer (August–September), as a result of post-reproductive altitudinal movements (Zamora 1990b, Jordano 1993). The mistle thrush does not overlap temporally with the ring ouzel, a long-distance migrant which uses these areas yearly as overwintering zones, remaining during the autumn and, depending on the extent and permanence of the snow, part of winter and spring (Zamora 1990a, Jordano 1993). During their stay in the juniper shrubland, both

bird species live almost exclusively on juniper fruits, and the droppings of *T. torquatus* and *T. viscivorus* are composed mainly (>90%) of juniper-fruit remains (fruit coat, pulp and intact seeds; Zamora 1990a, pers. obs.).

Methods

Experimental evidence of fruit rejection by birds

During the autumn of 1993 and 1994, we performed field experiments to determine the bird-rejection criteria for juniper fruits. The experiments consisted of offering frugivorous birds two different types of juniper fruits, experimental vs control, at the same time. We performed 5 different experiments, depending on the type of experimental fruit offered together with control:

Experiment 1. Effect of fruit ripening, in which experimental fruits were unripe green fruits at the end of the growing phase. We performed 1 trial for *T. torquatus* in 1994.

Experiment 2. Effect of fruit abortion. Fruits aborted during the fruit growing phase. 1 trial in 1994 for *T. viscivorus*, 2 trials in 1993 and 4 in 1994 for *T. torquatus*.

Experiment 3. Effect of pulp infestation by Carulaspis. Ripe fruits highly attacked by the pulp-sucker *Carulaspis* (5 or more scales per fruit, covering more than 50% of fruit surface). 1 trial in 1994 for *T. viscivorus*, 1 trial in 1993 and 4 in 1994 for *T. torquatus*.

Experiment 4. Effect of seed predation by Megastigmus. Ripe fruits attacked by seed-predator *Megastigmus*. 1 trial in 1994 for *T. viscivorus*, 3 trials in 1993 and 4 in 1994 for *T. torquatus*.

Experiment 5. Effect of high density of seed predation. This experiment was performed to test the effect that the density of *Megastigmus*-attacked fruits, with respect to unattacked fruits, exerts on fruit selection. For this, we doubled the number of *Megastigmus*-attacked fruits with respect to control fruits per dish. We performed 2 trials in 1994 for *T. torquatus*.

In all experiments, control fruits were ripe, unattacked and well-developed fruits. All fruits, whether experimental or control were collected from plants in the study area. Each experimental unit consisted of Petri dishes (8 cm diameter) exposed on the surface of large boulders that birds habitually used as perches, camouflaged with litter from the surrounding area and attached to the stone surface to simulate natural hollows. For each experiment, 10–15 experimental fruits of a specific fruit type together with the same number of control fruits were added per dish. Each dish was considered to be an experimental replicate, the number per trial being 7 for 1993 and 25 for 1994 (excepting to 15 dishes for Experiment 1 and 12 and 20 for Experiment 5). The variation in the number

of dishes between experiments was due to differences in the fruit availability in the area surrounding the experimental plot, depending on year, trial and fruit types. After 4–5 d, we recorded the number of fruits remaining in the dishes in each treatment (experimental vs control), under the assumption that fruits removed from dishes had been consumed by frugivorous birds. We detected no sign of fruit consumption or removal by rodents (easily identifiable by the type of remains left after fruit or seed manipulation) nor the presence of other frugivorous species and all the faeces found on the boulders, even within the dishes, belonged to *T. viscivorus* or *T. torquatus*. No fruits were found to have been displaced by wind or rain. In the 1993 experiments, we quantified the number of control and experimental fruits which appeared manipulated and rejected (with beak marks on their surface) in the dishes and surroundings. We detected no changes in the turgidity, colour or general features of fruits remaining in dishes during the exposure period in the experiment.

During the experiments, we repeatedly observed small groups (a minimum of 8 individuals) of both *T. viscivorus* and *T. torquatus* simultaneously eating fruits from dishes. Experiments for *T. viscivorus* were performed in September 1994, while for *T. torquatus* in October and November 1993 and 1994.

For each experiment, we calculated the fruit-removal rate as the proportion of fruits removed by birds from the dishes vs the initial number of fruits, for both experimental and control fruits. A significant difference in the removal rate between experimental and control fruits was interpreted as fruit selection.

Observational evidence of fruit rejection by *T. torquatus*

We compared the presence of fruit pests in a sample of fruits manipulated and afterwards rejected by *T. torquatus*, vs a sample of fruits from mother plants (see Manzur and Courtney 1984, for a similar procedure). Rejected fruits were identified by marks on the fruit surface left by a bird's beak, under the assumption that the fruits found under a plant belonged to that plant. In 1993 we determined the proportion of fruits attacked by *Megastigmus* in all rejected fruits lying underneath 20 plants ($n = 465$ fruits), as well as in a random count of 100 fruits per plant. The rejected fruits, together with a sample of fruits directly taken from each plant, were afterwards examined in the laboratory, recording fruit diameter (mm) and *Carulaspis* attack rate (mean number of scale insects per fruit, counting insect carcasses and signs of fallen scales). In 1994, we repeated the field survey for *Megastigmus* seed predation in rejected vs plant fruits in a sample of 13 plants ($n = 216$ rejected fruits).

Seed predation at seed rain stage

For four years (1992–1995), we collected seeds dispersed in bird droppings, noting the presence of *Megastigmus* exit holes. We also analysed the frequency of wasp presence in seeds directly taken from plants. The birds droppings gathered in the study area at the beginning of September were identified as belonging to *T. viscivorus*, while those collected in the same area during the October–November period proved to be from *T. torquatus*.

Statistical analysis

Data were analysed by non-parametric statistics. We used the Wilcoxon test to compare the *Megastigmus* attack rate, *Carulaspis* attack rate and fruit diameter between rejected fruits and fruits collected directly from plants. We used χ^2 test (two-tailed test) to compare: 1) the removal rate between experimental and control fruits in the field experiments, 2) the proportion of rejected fruits between experimental and control fruits in the experiments of 1993, pooling the results of all trials for each experiment and 3) the proportion of seeds depredated by *Megastigmus* among samples of seeds taken from plants and samples of seeds from bird droppings, for each year. All statistical analyses used in the present study were fixed to the standard significance level $\alpha < 0.05$ (Zar 1996). When statistically analysing more than one related variable, we chose the sequential Bonferroni adjustment for fitting the significance level (Rice 1989).

Results

Experimental evidence of fruit rejection by birds

Experiment 1. Effect of fruit ripening

In 1994, *T. torquatus* removed 83.11% of control fruits from dishes in this experiment, whereas only 1.78% of unripe fruits disappeared ($\chi^2 = 369$, $p < 0.0001$, $p < 0.05$ after Bonferroni, $n = 225$ fruits per treatment).

Experiment 2. Effect of fruit abortion

Aborted fruits were significantly less removed than control fruits by *T. viscivorus* (Fig. 1). Similarly, *T. torquatus* showed, in both study years, a general pattern of rejection of aborted fruits, removing significantly more control than aborted fruits in all but one trial of this experiment (Fig. 1).

Experiment 3. Effect of pulp infestation by *Carulaspis*

Fruits heavily infested by *Carulaspis* were significantly less consumed by *T. viscivorus* than were control fruits (Fig. 2). *T. torquatus* also significantly rejected pulp-

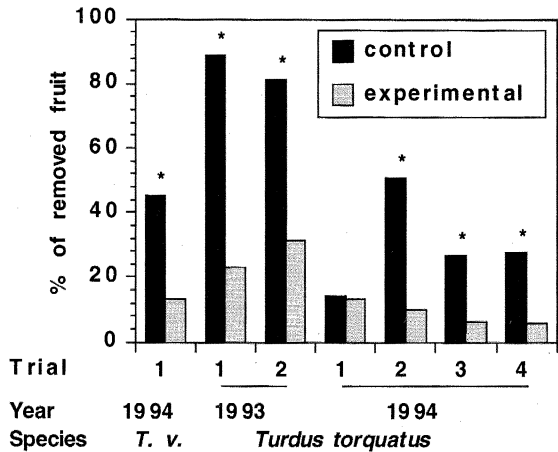


Fig. 1. Percentages of removed fruits (control vs experimental) in the experiment Effect of fruit abortion, differentiating trials, years and bird species (number of fruits per treatment: 225 *T. viscivorus*, 70 *T. torquatus* 1993, 375 *T. torquatus* 1994). The results of the χ^2 test comparing the proportion of removal between control and experimental fruits were 57.94 ($p < 0.0001$) for *T. viscivorus*, 67.23 ($p < 0.0001$) and 37.42 ($p < 0.0001$) for *T. torquatus* 1993, and 0.18 (n.s.), 158.26 ($p < 0.0001$), 61.46 ($p < 0.0001$) and 67.50 ($p < 0.0001$) for *T. torquatus* 1994 (* = $p < 0.05$ after Bonferroni).

sucker attacked fruits in both study years and in all but one trial of this experiment (Fig. 2). In the experiment with *T. torquatus* in 1993, we found 2.86% of fruits attacked by pulp sucker which have been manipulated and rejected by birds, but we found no control fruits rejected after manipulation ($\chi^2 = 2.80$, $p > 0.05$).

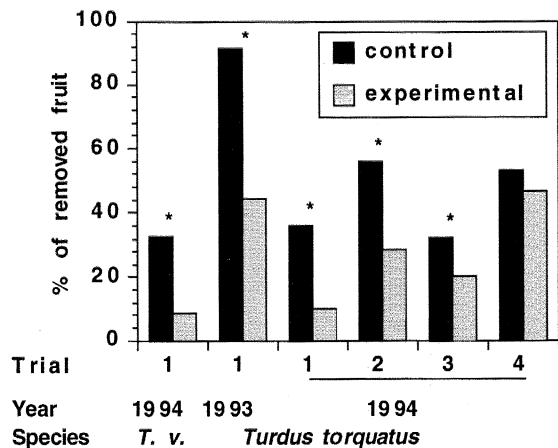


Fig. 2. Percentages of removed fruits (control vs experimental) in the experiment Effect of pulp infestation by *Carulaspis*, differentiating trials, years and bird species. The results of the χ^2 test comparing the proportion of removal between control and experimental fruits were 43.26 ($p < 0.0001$) for *T. viscivorus*, 38.74 ($p < 0.0001$) for *T. torquatus* 1993, and 72.12 ($p < 0.0001$), 23.29 ($p < 0.0001$), 14.02 ($p < 0.001$), and 2.34 (n.s.) for *T. torquatus* 1994. See also Fig. 1 for the number of fruits per treatment (* = $p < 0.05$ after Bonferroni).

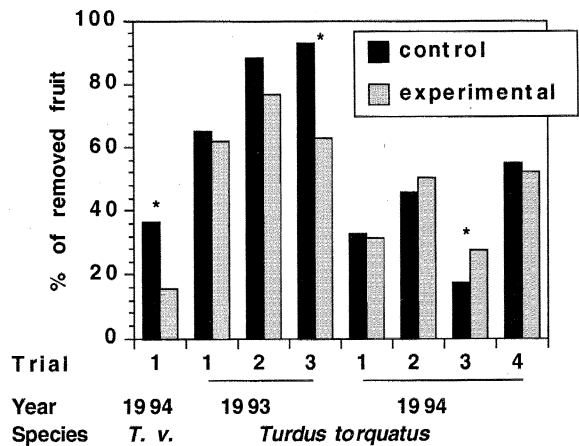


Fig. 3. Percentages of removed fruits (control vs experimental) in the experiment Effect of seed predation by *Megastigmus*, differentiating trials, years and bird species. The results of the χ^2 test comparing the proportion of removal between control and experimental fruits were 26.08 ($p < 0.0001$) for *T. viscivorus*, 0.14 (n.s.), 2.87 (n.s.) and 19.65 ($p < 0.0001$) for *T. torquatus* 1993, and 0.15 (n.s.), 1.36 (n.s.), 11.70 ($p < 0.001$), 0.44 (n.s.) for *T. torquatus* 1994. See also Fig. 1 for the number of fruits per treatment (* = $p < 0.05$ after Bonferroni).

Experiment 4. Effect of seed predation by *Megastigmus*

T. viscivorus showed a clear rejection pattern against seed-predator attacked fruits, the removal rate of these experimental fruits being significantly lower than for the control fruits (Fig. 3). *T. torquatus* tended to remove less *Megastigmus*-attacked fruits than control ones in 1993, whereas in 1994, with a lower overall fruit removal, no clear rejection pattern was evident. In 1993, we found that 13.16% of non-removed experimental fruits were actually manipulated and rejected close to the dishes, whereas this occurred in only 1.05% of non-removed control fruits ($\chi^2 = 24.7$, $p < 0.0001$).

Experiment 5. Effect of high density of seed predation

When the seed-predator attacked fruits were offered in double density with respect to control fruits, their proportion of removal by *T. torquatus* was significantly lower than for control fruits in the two trials of this experiment (Fig. 4).

Observational analysis of fruit rejection by *T. torquatus*

In 1993, the size of rejected fruits (6.01 ± 0.04 mm) was similar to the size of fruits which we collected directly from plants (6.16 ± 0.06 mm; $Z = -0.90$, $p = 0.37$, $n = 20$ plants, Wilcoxon test). In addition, we found neither unripe nor aborted fruits in the sample of fruits manipulated and rejected by *T. torquatus*. Pulp-sucker attack in the rejected fruit sample was similar to that in the collected-fruit sample in 1993 ($Z = -0.67$, $p = 0.50$,

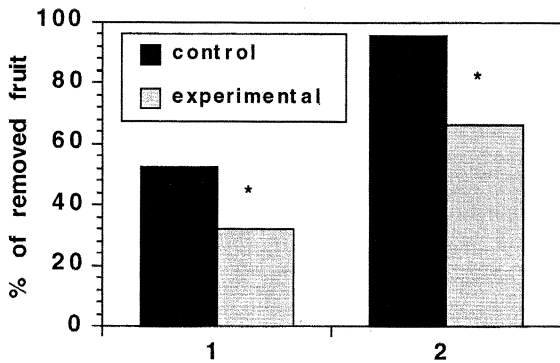


Fig. 4. Representation of the percentages of removed fruits (control vs experimental) in the two trials of the experiment Effect of high density of seed predation (number of control fruits: 120, 200). The results of the χ^2 test comparing the proportion of removal between control and experimental fruits were 13.89 ($p < 0.001$) and 75.44 ($p < 0.0001$; * = $p < 0.05$ after Bonferroni).

$n = 20$ plants, Wilcoxon test), with 2.07 ± 0.34 scales per fruit in collected-fruit sample and 1.69 ± 0.24 scales per fruit in the rejected fruit sample. On the contrary, the proportion of fruits attacked by the seed predator was significantly lower in the plants than in the sample of manipulated and rejected fruits, and most of the points in Fig. 5 lie above the line of the equation $y = x$ (1993: 47.48 ± 5.79 vs 65.27 ± 4.13 , $Z = -3.92$, $p < 0.0001$, $n = 20$ plants; 1994: 45.46 ± 5.39 vs 61.11 ± 4.53 , $Z = -2.87$, $p < 0.01$, $n = 13$ plants, Wilcoxon test). These field results agree with those found in the Experiment 4, in which more *Megastigmus*-attacked fruits appeared in the sample of manipulated and rejected fruits from the dishes.

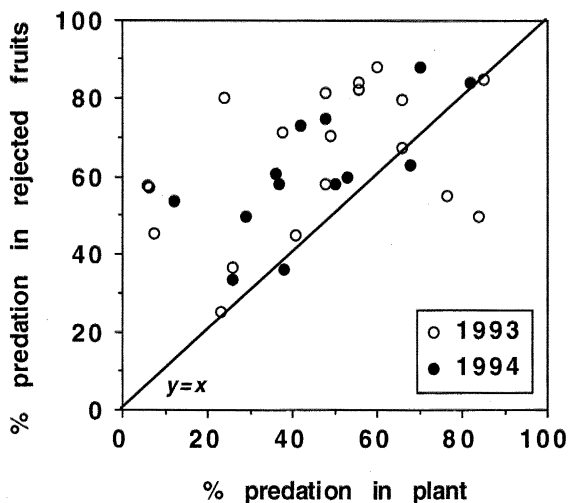


Fig. 5. Percentages of predation by *Megastigmus* in fruit samples with respect to the percentage of predation by *Megastigmus* in the sample of fruits rejected by birds and found underneath these plants ($n = 20$ plants in 1993 and $n = 13$ plants in 1994). The line representing the equation $y = x$ is also shown.

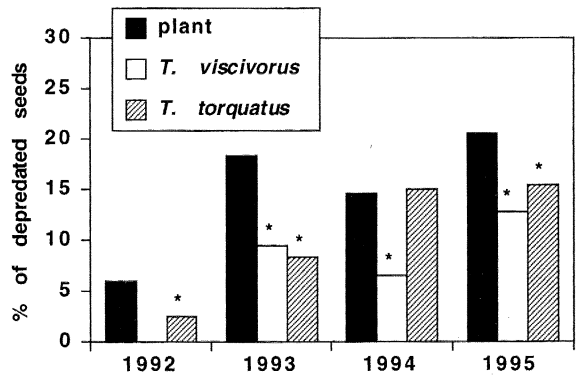


Fig. 6. Percentages of *Megastigmus*-depredated seeds in samples of seeds directly taken from plants and samples of seeds dispersed either by *T. viscivorus* or *T. torquatus* in different years (total number of seeds: 16205 plant sample, 5259 *T. viscivorus*, 10247 *T. torquatus*). The results of the χ^2 test comparing the proportion of depredated seeds between plant and bird sample, for each respective year, were for *T. viscivorus* 23.71 ($p < 0.0001$), 94.49 ($p < 0.0001$) and 76.82 ($p < 0.0001$; data not available for 1992), and for *T. torquatus* 11.31 ($p < 0.001$), 22.54 ($p < 0.0001$), 0.35 (n.s.) and 51.13 ($p < 0.0001$; * = $p < 0.05$ after Bonferroni).

Seed predation at seed rain stage

The seed rain from *T. viscivorus* and *T. torquatus* was more than 95% juniper seeds for all study years. The proportion of seeds depredated by *Megastigmus* was lower in the sample of seeds dispersed by birds than in the sample of seeds directly taken from the plants (Fig. 6). The difference between the two proportions was significant for *T. viscivorus* in all study years, and for *T. torquatus* in all but one year.

Discussion

Fruit selection by birds: consequences on seed rain

Our fruit-choice experiments and the rejected fruit sample showed that unripe and aborted fruits were strongly counterselected by the frugivorous birds. Unripe fruits differed strongly in colour and pulpiness from healthy ripe fruits, whereas the physiognomy of aborted fruits differed substantially from that of ripe fruits: lower pulp content, smaller size and shrivelled aspect. Thus, the bird response against unripe and aborted fruits signifies that the bird visually discriminates between fruits. These results agree with other studies demonstrating bird rejection of green and shrivelled fruits and the consumption exclusively of healthy ripe fruits (McPherson 1987, 1988, Allen and Lee 1992, Willson 1994).

Our experimental results for *T. viscivorus* and *T. torquatus* showed a similar trend in their response to fruits damaged by pests, consistently maintaining this fruit-rejection pattern between years. *T. viscivorus* re-

jected all damaged fruits at similar intensities, whereas *T. torquatus* rejected *Carulaspis*-attacked fruits more strongly than *Megastigmus*-attacked fruits.

The absence of fruits highly infested by *Carulaspis* showing beak marks suggests that these fruits were detected visually, like unripe and aborted fruits. In fact, the fruit heavily infested by *Carulaspis* become practically white coloured, being identified and rejected by birds without the need of handling within beak. Furthermore, highly infested fruits are smaller and with higher water content (García 1998). Other causes proposed for rejection of pulp-sucker infested fruits are that infestation can decrease pulp quantity, cause bitter flavours or encourage the presence of rot-causing microorganisms (Janzen 1977, Stiles 1980, Manzur and Courtney 1984, Courtney and Manzur 1985, Burger 1987, Jordano 1987, Borowicz 1988, Buchholz and Levey 1990). On the contrary, when juniper fruits had low *Carulaspis* infestation, birds did not differentiate them from healthy fruits, and thus consumed them. The fruits with low *Carulaspis* infestation are morphologically similar to uninfested fruits (García 1998). It is unlikely that the consumption of these fruits with some *Carulaspis* represents a significant protein supply, because many of the scales present on the green fruit fall before fruit ripening, and the ones that remain are dead when the fruit is eaten by the bird. The problem of obtaining extra protein imposed by a frugivorous diet is solved by *T. torquatus* and *T. viscivorus* by occasionally capturing small quantities of large ground arthropods, such as Myriapoda and Coleoptera (Zamora 1990a).

Numerous studies show that birds strongly reject fruits attacked by seed predators (Sork and Boucher 1977, Bossema 1979, Krischik et al. 1989, Traveset 1993, Traveset et al. 1995, Dixon et al. 1997, Hubbard and McPherson 1997; but see Scott and Black 1981). In most of these studies, bird discrimination was invariably associated with a marked contrast in fruit colour or morphology, enabling birds to select visually between attacked and unattacked fruits. On the contrary, the fruits attacked by *Megastigmus* did not differ either in colour or in morphology from healthy fruits (García 1998). This suggests that birds detect evidence of predation when manipulating the fruit in their beaks (selection level "within-beak", sensu Sallabanks 1993), but not visually. The rejection of fruits attacked by *Megastigmus* is probably due to the bird's detecting the residue of seed predation, and the excrement of the insect larvae, which are easily exuded when the fruit is manipulated (Manzur and Courtney 1984).

The comparison between the two types of experiments involving seed predation (equal density vs high density), suggests that the response against *Megastigmus*-attacked fruits depends on the abundance of seed predation in the fruit ensemble, given that higher proportions of attacked fruits promote stronger rejection behaviour (also see Manzur and Courtney 1984). Simi-

lar results have been found for *Carulaspis*, where only highly infested fruits were rejected. All of this suggests that the bird response against the pest is not always categorically acceptance/rejection of the fruit, but rather it is influenced by pest density.

Therefore, *T. viscivorus* and *T. torquatus* show two levels of selection: 1) visual, with respect to fruits that are green, aborted, and highly infested by *Carulaspis* (which fruit to pick); and 2) within-beak discrimination, which affects mainly fruits with depredated seeds (which fruit to swallow once picked). The fact that the selection against *Megastigmus*-attacked fruits is decided with the fruit inside the beak would explain why this discrimination is not as efficient as visual selection against the other damaged fruits, given that within-beak selection is the most labile level of selection in frugivorous birds (Sallabanks 1993).

The above described selective behaviour of birds has an important consequence on plant reproduction. The frugivores studied here reject two type of fruits: those highly infested by *Carulaspis* and most of those preyed upon by *Megastigmus*, which usually bear a lower proportion of viable seeds than unattacked fruits (García 1998). Moreover, they also reject aborted fruits which had no viable seeds at all. The result of this bird rejection is an improvement of the juniper seed rain, which contains a higher proportion of undamaged seeds than does the predispersal stock.

Potential of interaction between birds and pests

As consumers of the same resource, birds can compete with pests for the same fruits (Herrera 1984). It is evident that pests can reduce the quantity of healthy juniper fruits available for birds, since pests attack green fruits, whereas birds consume only ripe fruits. On the contrary, by eating ripe fruits, frugivorous birds do not decrease the amount of resources (green fruits) available to the insects.

From the point of view of the frugivorous bird, the rejection of attacked fruits implies that, to achieve the same quantity of resource, a greater effort in terms of search and handling time is needed (Manzur and Courtney 1984, Borowicz 1988, Buchholz and Levey 1990). In our case, however, most of the fruits that reach maturity are suitable to birds, because birds can consume a portion of *Megastigmus*-attacked fruits as well as almost all fruits with low *Carulaspis* infestation. In addition, the fruit crop can reach 400000 fruits/ha in years of medium to high production (García et al. 1996), and therefore birds have no problem in finding fruits. During low-production years, when competition between pests and dispersers could be more severe (Jordano 1987), there is no possibility of interaction because *Megastigmus* populations decline considerably (García 1997) and birds leave the juniper shrublands,

towards other areas of fruit at lower altitudes (*Crataegus monogyna*, *Lonicera arborea*, etc., Jordano 1993, pers. obs.). Therefore, the effects of pests on the fruit crop do not appear to be strong enough to bear population-level consequences for birds.

Apart from the bird-pest competition, birds, by consuming fruits can act as true predators of pests, with a potential impact on the populations of insect fruit predators (Herrera 1989, Toy et al. 1992, Traveset 1992). However, in this case, the seed predators, by abandoning the seeds before the fruits ripen, are not consumed by birds. Similarly, pulp-suckers attack green fruit and die before fruit ripen. Consequently, there are no population-level consequences of vertebrate frugivores for insects.

A further possibility is that the bird, by eating fruits, acts as a disperser of larvae inside the seeds, benefiting pests (Sallabanks and Courtney 1992, Nalepa and Piper 1994). However this does not occur in our system, because, again, the life cycles of *Carulaspis* and *Megastigmus* are out of phase with the activity of the birds. In any case, *Megastigmus* larvae do not enter prolonged diapause when the green fruit become ripe (Roques 1989, García 1998), and therefore it is not possible to transport seeds containing live larvae.

In conclusion, we find none of the three effects that frugivorous vertebrates could potentially exercise over fruit pests (competition, depredation or dispersal). In this case, frugivorous birds do not interfere with frugivorous insects. They have only a weak indirect interaction through rejection by birds of fruits attacked by pests.

Concluding remarks

The complete system, plant-pest-disperser, presented here shows that, despite the direct and indirect negative effects that pests have on juniper reproductive success, bird dispersers can offset predispersal interference and, through their fruit selection, increase the proportion of healthy seeds in the seed rain. The importance of this mutualism is reinforced by the large proportion of seeds removed from plants (only *T. torquatus* disperse more than 65% of the seed crop every year, 700000 juniper seeds/ha, García et al. 1996). Both qualitative (selective foraging) and quantitative (actual seed crop dispersed) factors, together with the temporal constancy in the bird assemblage (Zamora 1990a, b, Jordano 1993, García 1997), determine a predictable pattern in this plant-disperser mutualism. The consequence of bird fruit selection is the creation of a filtered seed bank composed almost entirely of juniper undamaged seeds.

By disseminating juniper seeds, *T. viscivorus* and *T. torquatus* can shape their own juniper shrubland habitat, reinforcing the mutualistic plant-seed dispersal as-

sociation in a positive feedback way (Herrera 1985, 1995). The resulting "habitat shaping" process is the consequence of an ecological fitting (*sensu* Janzen 1985) between species lacking a common history of interaction: the ancient, Tertiary relict junipers and the young, Pleistocene thrushes. This plant-seed disperser case in Mediterranean habitats exemplifies an efficient, ecologically based mutualism that does not require co-evolutionary adjustments.

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