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Fruit size in wild olives: implications for avian seed dispersal

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Summary

1. The response of frugivorous birds to an enlargement of fruit size, and the consequences for both birds and plants, are analysed for the interaction between avian seed dispersers and olives (*Olea europaea)*.
2. The enlargement of fruit size promotes a shift in frugivorous birds' feeding behaviour, from swallowing fruits whole to pecking pieces of pulp. The relative frequency of olive consumption using each feeding behaviour was assessed by combining field data on frequency of appearance of olive pulp and seeds with data from laboratory trials.
3. Sardinian Warblers (*Sylvia melanocephala*) and European Robins (*Erithacus rubecula*) were mainly peckers both on cultivated and wild olives. Blackcaps (*Sylvia atricapilla*) consumed wild olives mainly by swallowing but consumed cultivated olives (larger than the wild ones) primarily by pecking. Song Thrushes (*Turdus philomelos*) were primarily swallowers of both types of fruits.
4. Laboratory trials with Song Thrushes, Blackcaps and European Robins showed that: (a) all were able to peck fruits; (b) fruit size determined a shift from swallowing to pecking, as pecking frequency increased with the enlargement of the fruit size; (c) all the species had an increased fruit handling failure rate when trying to swallow increasingly large fruits; and (d) from the birds' perspective, small shifts in fruit size may have important consequences on fruit profitability.
5. Pecking on olives turns the mutualistic fruit–frugivore interaction into a fruit-pulp predator interaction, thus arising a conflict between the plant and frugivorous birds.
6. This study shows that heavy dependence on fruit is not always simply related to seed dispersal. The same frugivorous bird species can act as a seed disperser or a pulp predator for the same plant species. The threshold between these roles is highly influenced by the ratio gape size/fruit size.

Key-words: Frugivorous birds, fruit feeding behaviour
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Introduction

Frugivorous birds in the Mediterranean basin may disperse seeds using two different feeding behaviours: swallowing the fruit whole or pecking pieces of pulp.

Swallowing is the common behaviour of frugivorous seed dispersers in the Mediterranean basin (Herrera 1984a) and most of the fleshy-fruited plants in the region rely on this bird feeding behaviour to disperse their seeds (Herrera 1984b, 1995). This mutualistic system can only occur if, to some extent, fruit size and gape width adjust each other (Herrera 1984a; Wheelwright 1985; Debussche & Isenmann 1989). Seed dispersal may become difficult for plant species showing such a high variation in fruit size that some of their fruits cannot be swallowed by some bird species (Rey 1992; Wheelwright 1993). This variation may occur among and/or within individual plants (Jordano 1984; Wheelwright 1993; Herrera *et al*. 1994; Obeso & Herrera 1994; Jordano 1995).

Feeding on large Mediterranean fruits, such as those dispersed by mammals (Debussche & Isenmann 1989; Herrera 1989), is not a problem for small frugivorous birds accustomed to peck on fruits (gulping chunks of pulp instead of swallowing the fruit whole). Pulp pecking may allow the dispersal of small seeds from large multiseeded fruits such as *Arbutus unedo*, *Ficus carica*, *Punica granatum*, *Fragaria vesca* and several species of *Morus*, *Rubus* and *Opuntia* (Thomas 1979; Jordano 1981, 1982, 1984; Herrera 1984b; Bronstein & Hoffmann 1987). However, seed dispersal may be seriously limited if seeds are too large to be ingested while pecking. This feeding behaviour provides additional advantages for birds as they do not carry the ballast of the seed and most of their gut volume can be used for processing digestible material (Sorensen 1984; Levey 1986, 1987; Worthington 1989; Levey & Grajal 1991).

As a result of both feeding behaviours outlined above, one bird species may act as a seed disperser by swallowing some fruit species and/or by pecking others (see Jordano 1982; Herrera 1984b; Snow & Snow 1988). Furthermore, we would expect that birds would probably peck those fruits that were too large for swallowing instead of rejecting them. We would also expect that when a fruit species shows a fruit size range wider than that swallowable by birds, birds will swallow some fruits (acting as seed dispersers) and will peck others (acting as pulp predators). There is still another possibility as ‘pecking birds’ carry the fruit in their bill from the parent plant to another place, thus dispersing seeds but not by ingestion (M. Debussche, personal communication).

We will analyse the consequences, both for the birds and the plants, of fruits that are too large for birds to swallow. Two approaches are used. First, the interactions of avian fruit consumers with wild olives and with a larger cultivated variety are compared. Second, the effect of fruit size on birds’ feeding behaviour and fruit handling success is experimentally analysed.

The commercial olive (*Olea europaea* var. *europaea*) is a cultivated variety of the wild olive (*Olea europaea* var. *sylvestris*), which is one of the main winter fruiting plants in the Mediterranean shrubland of southern Spain (Herrera 1984b; Jordano 1987a). The fruits of the wild variety are single-seeded elliptical drupes attached at one end, with sizes that most of frugivorous birds can swallow and consequently disperse seeds (Jordano 1987a; Rey 1992). However, fruit size of commercial olives has been increased via artificial selection, resulting in fruits too large to be swallowed by most frugivores (Rey 1992, 1993). These birds consume cultivated olives by pulp-pecking (Tutman 1969; Tejero, Camacho & Soler 1983; Rodríguez de los Santos, Cuadrado & Arjona 1986; Debussche & Isenmann 1990; Rey & Gutiérrez 1996). This system constitutes a valuable opportunity to test the predictions formulated above by comparing the feeding behaviour of frugivorous birds on cultivated olive trees (‘experimental’ conditions) and wild olive trees (‘control’).

Specifically, the following questions are addressed. (a) How do birds respond to an enlargement in fruit size? (b) What is the relative frequency of pecking and swallowing behaviour by frugivorous seed dispersers for cultivated and wild olives? (c) What is the proximate cause of pecking behaviour by seed dispersers? (d) What are the consequences for seed dispersal of wild olives?

Methods

FREQUENCY OF FRUIT SIZES AND PECKING BEHAVIOUR IN THE FIELD

The size of olive fruits was estimated in four olive orchards (6–9 km^2 each) and in a wild olive shrubland, all located in the Guadalquivir Valley, southern Spain (see Rey 1995). The maximum width (second-largest dimension) was measured on 60 fruits from each of 10 cultivated olive trees per plot and from each of 40 wild olive trees in the wild olive shrubland. These 40 trees were not exactly the same individuals each season because the set of fruit-bearing trees differed between years. Based on these data and on the gape width of birds from the same region (data from Herrera 1984a), the percentage of fruits small enough to be swallowed by the four most abundant frugivorous bird species in the plots (Blackcap, Song Thrush, Sardinian Warbler and European Robin; see Rey 1993, 1995) was estimated. Fruits were considered to be swallowable if their width was less than or equal to the birds’ gape width (see Herrera 1984a; Wheelwright 1985; Jordano 1987b; Snow & Snow 1988). Although measuring gapes on museum specimens or live birds probably underestimates maximum gape width (as it does not consider its flexibility), data from Mediterranean sylviid warblers (Jordano 1987b) and our laboratory observations indicate that these birds rarely swallow fruits wider than their gape.

During two autumn–winter seasons (1989–90 and 1990–91), Blackcaps, Song Thrushes, European Robins and Sardinian Warblers were mist-netted in the same plots used to determine the frequency of fruit sizes. Birds were retained in cloth bags until they defecated and, additionally, their digestive tracts were flushed with a saline solution of 1% NaCl (Moody 1970; Herrera & Jordano 1981). Defecations and digestive contents will be referred to as ‘diet samples’ hereafter. Diet samples were analysed using the procedure described by Herrera & Jordano (1981), which takes into account the presence of epicarp, pulp and seeds of fruits. The frequency of occurrence and proportion of olive pulp in the diet were determined along with the frequency of appearance of olive seeds.

Indirect estimates of the frequency of pecking behaviour relative to swallowing were obtained based on the ratio ‘number of diet samples with olive seeds/number of diet samples with olive pulp’ (swallowing index, SI hereafter) found in birds captured in olive orchards and the wild olive shrubland plot. SI ranges between 0 and 1; with low values indicating a high frequency of pecking and high values suggesting a high frequency of swallowing. This index suffers a possible shortcoming as some bird species usually regurgitate large seeds (Herrera 1984a; Sorensen 1984; Johnson *et al.* 1985; Levey 1986; Worthington 1989; Levey & Grajal 1991). Birds species that regurgitate will show a smaller SI than species that do not. However, SI is suitable in our study for several reasons: (1) laboratory observations show that European Robins, Song Thrushes and Blackcaps almost always regurgitate rather than defecate the seeds of both wild and cultivated olives. Thus, the effect of regurgitation on SI is likely similar among species. Although we have no information about Sardinian Warblers, we believe that it regurgitates the seeds owing to the small size of this species compared with the size of the seeds (Levey 1986); (2) the differences among species reflected by the SI are so high that it would tolerate some bias without changing the conclusions arising from the interspecific comparisons; (3) as will be shown in the results, there is consistency, within species, between the relative pecking frequency reflected by SI and the results obtained during laboratory trials; (4) finally, it would be expected that the importance of olives in the diet would be lower for peckers than for swallowers. This expectation agrees with the results obtained with the SI.

To assess the relative importance of pecking in relation to fruit removal on wild olives in the field, four branches were tagged on each tree (n = 40) and their fruits were counted fortnightly from October (the beginning of the ripening period) to March (when most fruits dry up). At every count, the number of ripe, unripe, damaged (but not pecked) and pecked fruits were recorded. Fruit removal rates and the incidence of fruit pecking for every branch was calculated based on these data, obtaining an average value for each tree. Fruits were classified as removed by birds only if they disappeared from the branch ripe and undamaged, because the seed dispersers involved in this study reject infested fruits (e.g. Jordano 1987a). To take into account the effect of fallen fruits on estimated removal rates, fortnightly corrections were made based on the fruits present in four 25×25 cm^2 quadrats beneath each tree. Fruit removal was not estimated in olive orchards because: (1) the large size of the fruits generally precludes fruit removal by birds (Rey 1992) and (2) additionally, the large crops produced by each tree make very difficult to detect very occasional removal. To measure the incidence of pecking behaviour on cultivated olives, by the end of the season and after harvest by humans, all fruits on the tree and on the ground beneath 25 trees in each plot, were counted, noting the percentage of pecked fruits.

EXPERIMENTAL TRIALS OF WILD OLIVE PECKING

Mist-netted Blackcaps, European Robins and Song Thrushes were maintained individually in holding cages ($40 \times 40 \times 40$ cm^3). Room light and temperature were similar to outdoors conditions. The birds' diet consisted on commercial food for insectivores, fruit (mainly olives, wild olives and *Pistacia lentiscus* fruits) and mealworms. Water and food were available *ad libitum*. Birds entered experiments at similar body mass to that of capture.

The following laboratory trials were carried out to test whether these frugivores, which normally disperse seeds, peck wild olives and to elucidate the role of fruit size in feeding behaviour. Three fruit size categories were defined based on the natural width range of wild olives (6·7–11·1 mm, n = 40 trees): small fruits (< 7·0 mm), medium sized fruits (7·0–9·0 mm) and large fruits (> 9·0 mm). In each experimental trial a single fruit of a size category was offered, and the feeding behaviour (swallowing or pecking) used by the birds was noted. These trials were conducted with two Song Thrushes, six Blackcaps and three European Robins. Each fruit size class and individual bird combination was repeated 10 times (30 trials/individual). The percentage of trials in which the fruit was pecked by each individual was used to obtain an average value for each species.

FRUIT HANDLING SUCCESS

To calculate birds' fruit handling success on wild olives, fruits were hung from holders suspended above a perch. Four Song Thrushes, five Blackcaps and two European Robins were used. Whether fruits were swallowed or dropped was noted. At least 30 handling attempts for each fruit size class and individual bird combination were analysed.

To estimate frequency of unsuccessful handling in the field, a random subset of 16 trees was monitored; the same method was used for correcting removal rates but in this case the fallen fruits were classified as abscised or dropped by birds based on whether beak marks were on the fruit. Ripe fruits with beak marks were considered unsuccessfully handled fruits (Sallabanks 1992, 1993; P. Jordano, personal communication).

STATISTICAL ANALYSES

Data from laboratory trials were included, after arcsin transformation (Zar 1984), in two separate repeated measures ANOVA to test for differences in pecking frequency and fruit handling success among species and fruit sizes. In both analyses, the repeated measure (within-subject effect) was fruit size, species being the between-groups effect. A repeated measures analysis was used because each bird was tested with the three fruit size classes, and thus data obtained for each size by each individual bird are not independent. This analysis requires sphericity and compound symmetry (Dixon 1988), besides normality and homoscedasticity. Specifically, the univariate approach of the analysis was used because if the assumptions about sphericity and compound symmetry are met, the univariate approach is more powerful than the multivariate one, especially in small samples (Dixon 1988). Sphericity was tested for using Mauchley's test and compound symmetry was corrected for using Greenhouse–Geisser and Huynh–Feldt adjustments

(Dixon 1988). These two assumptions and the equality of variances (tested using Bartlett's test) were accomplished by our data set (tests not shown). Furthermore, the univariate approach is less sensible to the assumption of multivariate normality than the multivariate one. As the number of observations in each cell of the statistical design was small normality was tested for using the method described in Sokal & Rohlf (1981, p. 413). Our dependent variables were normally distributed (Kolmogorov–Smirnov, $P > 0{\cdot}05$) for each level of the within-subject effect (with the single exception of the small fruit size level in the analysis of the percentage of pecking). Notwithstanding this exception we prefer to keep this analysis because ANOVA is a robust test regarding normality, and because any other alternative non-parametric test (e.g. Friedman test, see Zar 1984) would not allow us to test for significance of each effect (i.e. fruit size, bird species and interaction effects). Unless otherwise stated, all data are presented as means ± 1 SD.

Results

FREQUENCY OF SWALLOWABLE OLIVES

Variation in frequency of swallowable olives for Song Thrushes and Blackcaps has been provided elsewhere (Rey & Gutiérrez 1996). Briefly, mean fruit width was 15·65 ± 1·47 mm in olive orchards, and 6·86 ± 1·39 mm in wild olive shrubland. The mean frequency of fruits small enough to fit the Blackcap's gape ranged between 0 and 2·0% in olive orchards (n = 4 orchards/year × 2 years/orchard = 8). In the wild olive shrubland this frequency was 58% in 1989–90, and 88% in 1990–91. These values ranged between 2 and 74% for Song Thrushes in olive orchards, whereas all the fruits in the wild olive shrubland were small enough to be swallowed. For European Robins, the values ranged between 0 and 1% in olive orchards and 35–79% in the wild olive shrubland. Finally for Sardinian Warblers, no fruits were small enough to be swallowed in olive orchards and values ranged between 13 and 58% in the wild olive shrubland.

FREQUENCY OF PECKING BEHAVIOUR

The four frugivorous bird species frequently consumed olives; 65·8–100% of diet samples contained olives, see Table 1. Moreover, olives represented a very important fraction in the diet both in olive orchards and in wild olive shrublands. Thus, SI is probably a good estimate of the frequency of pecking behaviour. Based on SI, Sardinian Warblers and European Robins are peckers both in olive orchards (SI = 0 and 0·06, respectively) and wild olive shrubland (SI = 0 and 0·12, respectively). Moreover, these two species showed no significant differences in the proportion of their diet samples containing seeds between habitats ($\chi^2 = 1{\cdot}17$, $P > 0{\cdot}05$, in the case of European Robin). Blackcaps consumed cultivated olives primarily by pecking (SI = 0·05), but wild olives primarily by swallowing (SI = 0·58). This difference was significant ($\chi^2 = 234{\cdot}19$, $P < 0{\cdot}001$). Finally, Song Thrushes were primarily swallowers in wild olive scrubland (SI = 1), and also swallowed frequently in olive orchards (SI = 0·49), although still significantly less often (Fisher exact test, $P < 0{\cdot}05$) than in the shrubland.

Feeding behaviour seems to influence the amount of olive included in the diet. Table 1 shows a lower importance of wild olives in the diet for Sardinian Warblers and European Robins, which primarily peck, than for Blackcaps and Song Thrushes, which primarily swallow. Overall, pecking birds seem less attracted to wild olives than birds prone to swallow.

EFFECTS OF FRUIT SIZE ON FEEDING BEHAVIOUR ON WILD PLANTS

Pecking wild olives is a common behaviour, at least for two of the three bird species tested in captivity. Pecking frequency varied significantly among bird species and fruit sizes (see Table 2). Trials with different fruit size classes clearly showed that smaller birds pecked more frequently. European Robins often pecked wild olives (55·0 ± 23·2% of the trials), especially medium and large fruits. In contrast, Song Thrushes rarely pecked (6·7 ± 9·4%), and solely large fruits. Blackcaps also frequently pecked fruits, pecking a higher proportion of the larger ones

Table 1. Occurrence of olives in the diet of frugivorous birds

	Wild olive shrubland					Olive orchards				
Species	% Volume	% Olive	% Seeds	SI	N	% Volume	% Olive	% Seeds	SI	N
Sardinian warbler	28·4 ± 8·2	91·7 ± 6·2	0	0	14	25·4 ± 4·1	92·3 ± 7·15	0	0	26
European robin	17·4 ± 3·7	65·8 ± 4·3	4·3 ± 4·3	0·12	38	39·9 ± 5·9	90·7 ± 3·3	1·8 ± 1·8	0·06	114
Blackcap	65·7 ± 2·3	95·1 ± 5·0	55·0 ± 1·1	0·58	271	41·7 ± 3·6	90·5 ± 2·6	3·6 ± 2·0	0·05	485
Song thrush	72·6 ± 12·1	100 ± 0·0	100	1	5	58·1 ± 8·1	86·0 ± 3·0	36·1 ± 11·1	0·49	104

%Volume = volume (%) of the diet represented by olives; % Olive = diet samples containing olive remains (%); % Seeds = diet samples containing olive seeds (%). Data for these three parameters are averaged among plots and years (mean ± 1 SE; n = 8 for olive orchards and 2 for the wild olive shrubland). SI = swallowing index (see text), that refers to N (number of diet samples containing olive remains).

(37·2 ± 25·1%). The non-significant interaction effect yielded by the ANOVA indicates a consistent tendency among bird species to increase frequency of pecking behaviour with increased fruit size.

Note that the relative frequency of pecking among these captive birds agrees closely with that found by the SI, which was based on field data.

WILD OLIVE HANDLING SUCCESS

Fruit handling success varied significantly among bird species and fruit sizes. The ANOVA analysis also yielded a significant interaction effect; thus the increase in fruit size influenced each species' handling success differently (Table 3). European Robins were able to handle only small fruits successfully (58·3% of successful attempts with this size class). Blackcaps dropped high percentages of fruits in the medium and large size classes, only obtaining a high percentage of successful attempts with small fruits (67·7%). The most efficient bird was the Song Thrush with more than 50% success for small and medium sized fruits, and 34·9% for large fruits.

Wild olive handling seemed difficult for small frugivorous birds such as the Blackcaps and European Robins because of the size and elliptical shape of the fruits. After picking fruits from the holder, these birds normally hit them on the perch to position them properly for swallowing; however, during such manipulation, they frequently dropped fruits.

Our experimental data fit those from the field; unsuccessful handling was a frequent way of fruit loss for wild olive trees. The percentage of fruit loss due to handling failure ranged between 0 and 60% (average 8·51 ± 15·51%, n = 16 trees). This percentage was significantly correlated with fruit size (r_s = 0·64, P < 0·01, n = 16, see Fig. 1), as expected from the laboratory trials.

Table 2. Pecking behaviour: percentage of trials in which the fruit was pecked

Species (gape width)	*N*	Fruit Size Small (< 7 mm)	Medium (7–9 mm)	Large (> 9 mm)	Total
European Robin (8 mm)	3	34·7 ± 16·2	69·1 ± 27·0	92·8 ± 6·3	55·0 ± 23·2
Blackcap (8·5 mm)	6	8·3 ± 20·4	12·1 ± 9·5	37·2 ± 25·1	17·6 ± 16·9
Song thrush (13·7 mm)	2	0	0	11·8 ± 16·6	6·7 ± 9·4

Effect	Repeated measures ANOVA *F*	df	*P*
Species	18·59	(2, 8)	0·001
Fruit size	5·50	(2, 16)	0·01
Interaction	0·45	(4, 16)	0·77

Data are means ± 1 SD. *N* = number of birds. Gape width data from Herrera (1984a). The results of repeated measures ANOVA test (see Methods) accounting for the effects of bird species and fruit size on the frequency of pecking behaviour are also shown.

Table 3. Handling success: percentage of trials in which the fruit was successfully handled for swallowing

Species (gape width)	*N*	Small (< 7 mm)	Medium (7–9 mm)	Large (> 9 mm)
European Robin (8 mm)	2	58·3 ± 11·8 (50·0–66·7)	0·0 ± 0·0	0·0 ± 0·0
Blackcap (8·5 mm)	5	67·7 ± 18·8 (45·9–78·9)	36·1 ± 19·6 (24·7–58·7)	11·7 ± 16·2 (0·0–33·3)
Song thrush (13·7 mm)	4	61·5 ± 17·0 (37·5–77·6)	56·7 ± 8·4 (51·0–66·4)	34·9 ± 11·3 (24·1–50·0)

Effect	Repeated measures ANOVA *F*	df	*P*
Species	13·33	(2, 8)	0·003
Fruit size	33·95	(2, 16)	<0·0001
Interaction	5·25	(4, 16)	0·007

Data are means ± 1 SD. Range is expressed in parentheses. *N* = number of birds. The results of repeated measures ANOVA test (see Methods) accounting for the effects of bird species and fruit size on handling success are also shown.

INTENSITY OF PECKING ON CULTIVATED AND WILD OLIVES

In olive orchards it was common to observe pecked fruits both on tree branches and on the ground. By the end of the season and after the harvest, pecked fruits made up 20·3 ± 16·8% (range 2–51%) of the olives remaining on the trees and 14·7 ± 6·8% (range 4–33%) of the olives found on the ground (note that these percentages are not relative to the total crop initially produced by the trees). In the wild olive shrubland, 50% of trees showed pecked fruits on tagged branches. Pecked fruits made up 0–9·54% of fruits on branches (averaging 1·90 ± 2·85%, n = 40 trees) (although other non-disperser species may contribute to this percentage, i.e. Great Tit *Parus major*, and Blue Tit *Parus caeruleus* that consume small amounts of olives by pecking; Jordano 1987a; P. J. Rey, unpublished observations); whereas in the same plot the mean fruit removal was 24%. That is, on average there was 1 pecked fruit per 12 dispersed seeds. There was a significant correlation between mean fruit size of the tree (estimated as fruit width) and percentage of pecked fruits on branches (Spearman, r_s = 0·37, P < 0·05, n = 37 trees), suggesting that, also in the field, large fruits were more intensively pecked than small fruits.

Discussion

Wild olive trees have large intraspecific variation in fruit sizes. The fruits of many individuals are larger than the gape size of the small frugivorous birds that usually disperse seeds of Mediterranean fleshy fruited plants. This paper shows that some bird species are able to develop an 'illegitimate' feeding behaviour if compared with their usual role as seed disperser frugivores: pecking large fruits to extract pulp. This illustrates that what is in the best interest of frugivorous birds is frequently not in the best interests of the plants, and vice versa (Snow 1971).

EFFECTS OF FRUIT SIZE ON FEEDING BEHAVIOUR

In the present study, fruit size has two major consequences from the bird's perspective. First, it affects fruit profitability because it influences fruit handling success and handling time before swallowing (Rey & Gutiérrez 1996); subtle changes in fruit size can substantially increase or decrease handling success. For instance, in the case of Blackcaps, an enlargement of 2 mm in fruit diameter of swallowable fruits almost doubled the failure rate in fruit handling (see Table 3). Second, variation in fruit size promotes changes in feeding behaviour. Our study shows that fruit size determines the change from swallowing to pecking behaviour. This is also influenced by bird size: the smaller the bird, the smaller the fruit size at which this transition in behaviour will occur. This observation is supported by data from olive orchards, where the large size of the olives causes a high frequency of pecking by all the bird species. The increase of fruit diameter poses some other consequences for birds out of the scope of this paper, such as a larger amount of net pulp ingested (if the bird could swallow the fruit whole), an increase of the pulp–seed ratio in the case of single-seeded species (Jordano 1987b, 1992), or a variation in processing rate in the gut (Levey 1987).

What is the proximate cause that accounts for the change in feeding behaviour from swallowing to pecking? This study shows that birds frequently failed when handling large fruits. Similar findings have been reported elsewhere (see Salomonson & Balda 1977; Wheelwright 1985; Sallabanks 1992, 1993). In our study, the high frequency of unsuccessful attempts to swallow wild olives might explain why birds often pecked them.

Our results suggest that pecking is an opportunistic strategy that allows small birds to exploit a wider range of fruits than if they would only swallow them. The high energetic reward of olives (Rey 1992) probably offsets the expense of pecking and permits the ingestion of sufficient energy to make the behaviour cost-effective (Rey & Gutiérrez 1996). This strategy also allows birds to increase their range of profitable resources, so that they can inhabit places otherwise inadequate (i.e. cultivated olive orchards, Rey 1993). Nonetheless, the increased cost of pecking might result in a larger relative frequency of small sized frugivores in the wild olive shrubland than in olive orchards (Rey 1993). In particular, the smaller species considered in this study (Sardinian Warbler and European Robin) are very scarce in olive orchards, whereas the larger ones (Blackcaps and Song Thrushes) are abundant in this habitat (Rey 1993).

CONSEQUENCES FOR THE PLANT OF PECKING

The change from swallowing to pecking behaviour on wild olives turns the mutualistic fruit-seed disperser interaction into a fruit-pulp predator interaction. The consequences for the plant will depend on the fruit size/bird size relationship; small frugivores faced with slight enlargements on fruit size could easily become pulp predators.

This paper suggests that more caution is needed when classifying a bird as a seed disperser for a given plant species, or more generally, for most of the fleshy-fruited species of an area. Although a particular bird can disperse some seeds of a certain plant species, it may also peck some fruits. Indeed, the possibility exists that the bird might act as a pulp predator more frequently than as a seed disperser. This seems to be the case with the interaction between wild olives and European Robins and probably Sardinian Warblers. Additionally this paper shows that, although some birds mainly act as seed dispersers, it is also important to consider their efficiency (Schupp 1993). For example, Blackcaps are known to be the major wild olive dispersers (Jordano 1987a; Rey 1992), but this study shows that they frequently fail to swallow fruits that they handle, leaving many seeds undispersed (see also Salomonson & Balda 1977; Wheelwright 1985; Sallabanks 1992, 1993).

The change of feeding behaviour described in this paper and its consequences for plants in natural systems have been neglected until now. Therefore, this study adds another degree of complexity to the fruit–frugivore interaction (see also Levey 1987; Sallabanks & Courtney 1994). The same frugivorous bird species could act as seed dispersers or pulp predators for different plant species, and even more for different individuals of the same plant species, as variability in fruit size can be frequently higher at an inter-individual

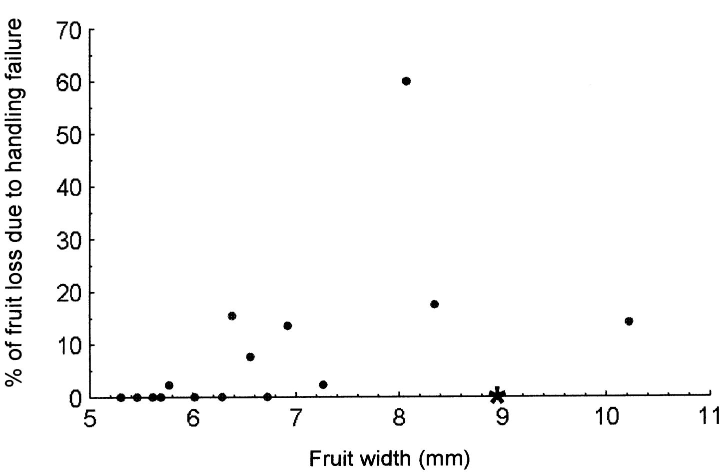

Fig. 1. Relationship between fruit losses due to handling failure and fruit size (field data). Percentages are referred to the total amount of fruit lost. The asterisk indicates a tree that achieved only 3% of fruit removal along the season, suggesting a low visitation rate and thus a negligible percentage of fruit loss due to handling failure.

level than at an intra-individual one (Obeso & Herrera 1994; but see Wheelwright 1993; Jordano 1995); the threshold between both habits would be in some extent set by the ratio of bird size/fruit size.

Finally, this paper illustrates an example of an interaction at the limit: conflicting selection pressures on fruit size arising because some fruits exceed birds' gape width. This can provide us some cues about the evolution of fruit size. We have not found any information testing specifically the heritability of olive fruit size. Recent evidence obtained from cultivated varieties shows that fruit size is the morphologic character best related to genetic similarity among cultivars (Fabbri, Hormaza & Polito 1995), which suggests a high heritability of fruit size. As small frugivores dominate the guild of avian seed dispersers in the native Mediterranean shrubland (Herrera 1984b), a strong selective pressure favouring small fruit sizes could be acting nowadays. However, large birds of native shrublands (corviids, starlings and especially thrushes), that can swallow even the largest wild olives, could also benefit individual plants with large fruits, thus keeping the high variability of wild olive fruits.

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