



Small-scale spatial variation in the interactions between *Prunus mahaleb* and fruit-eating birds

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Abstract

We studied fleshy fruit consumption by birds on individual *Prunus mahaleb* trees in four plots in northwestern Spain. We found large variation among trees in the relative contribution of different bird species to fruit removal. This variation, which occurred on a scale of meters, was correlated with the distance from the tree to nests of *Phoenicurus ochruros*, a major fruit consumer, and with the kind of microhabitat surrounding each tree. In the four plots studied, trees located farther away from *P. ochruros* nests received relatively fewer visits by this species, and relatively more by *Turdus merula* and *Sylvia atricapilla*. These three main consumer species differed in the kinds of microhabitats (rocks, loose stones, bare or grassy soil, and woody vegetation) where they flew after visiting *P. mahaleb*, and thus they probably created different patterns of seedfall. This study adds to the evidence that environmental factors extrinsic to plants, and acting at different spatial scales, greatly influence the identity of the fruit consumers visiting individual trees. This influence undermines the chances that fruit traits become evolutionary modified so as to attract those consumers providing the “best” seed dispersal services to the plants.

Introduction

In animal-dispersed plants, natural selection should favor the evolution of traits that enhance fruit removal by those fruit consumers that provide the best seed dispersal services (Snow 1971; McKey 1975; Howe and Estabrook 1977). However, the set of animal species visiting fleshy-fruited plants at a given place and time depends not only on heritable plant traits (such as pulp and seed characteristics) that influence fruit choice, but also on habitat characteristics that affect the relative abundances of animal species and their foods (Fuentes 1995). All else being equal, the potential for adaptive evolution of fruit traits depends on the extent that differences in seed dispersal success are due to genotypic, as opposed to purely environ-

mental, differences among individual plants (Herrera 1986).

Several studies have found important variation in the composition of avian frugivore assemblages among populations of the same plant species (McDiarmid et al. 1977; Howe and Vande Kerckhove 1979; Bronstein and Hoffmann 1987; Fuentes 1995; Pizo 1997). This kind of spatial variation can frequently be attributed to specific environmental correlates of bird abundance across habitats, landscapes and geographical areas (Jordano 1993, 1994). A few studies document variation in the identity of fruit consumers among individual plants (Snow and Snow 1984, 1988; Traveset 1993, 1994; Katusic Malmborg and Willson 1988; Sargent 1990; Jordano and Schupp 2000), but, to our knowledge, only Traveset (1993,

see also 1994) related it in a quantitative way to specific causes.

In *Prunus mahaleb* L. (*Rosaceae*), a treelet that produces fleshy fruits, variation of avian frugivore assemblages has been documented at the temporal scale of years (Jordano 1994), as well as at three spatial scales - among distant localities (Gutián et al. 1992; Jordano 1994), among habitats within localities (Gutián et al. 1992; Jordano 1994; Herrera and Jordano 1981; Schupp 1993) and among individuals within habitats (Herrera and Jordano 1981; Jordano and Schupp 2000). Here we document spatial variation of the frugivore assemblage (proportion of fruits taken by each bird species) among individual *P. mahaleb* trees growing next to each other. Then, we explore connections between this variation and the spatial heterogeneity of habitat characteristics and bird activity. Specifically, we address whether the proportional contribution of different bird species to fruit removal is related to the distance from trees to nests of *Phoenicurus ochruros*, a major fruit consumer. Finally, we examine how the identity of fruit consumers might affect the fitness of individual trees, as the bird species that feed on *P. mahaleb* differ in the way they handle fruits (Herrera and Jordano 1981; Gutián et al. 1992; Jordano 1994; Rodríguez and Bermejo 1995; Jordano and Schupp 2000), and also in the patterns of seedfall they create (Herrera and Jordano 1981; Schupp 1993; Jordano and Schupp 2000).

Methods

Herrera and Jordano (1981), Gutián et al. (1992), Schupp (1993), Jordano (1994, 1995) and Jordano and Schupp (2000) give details on the natural history of *P. mahaleb* and its interaction with vertebrate frugivores.

We selected two *P. mahaleb* populations for our study, one in Portela (P, which was also studied by Gutián et al. (1992)) and one in El Estrecho (E). These two sites are about 3 km apart, near the Penarubia Dam, northwestern Spain (42°30'N 6°51'O, at 500–600 m asl). Both consist of steep rocky slopes that extend from the base of vertical limestone cliffs, which are mostly devoid of vegetation, down to riverine woodlands. These slopes are vertically traversed by shallow ravines. The long middle axis of each ravine is covered with loose stones, and the humps between adjacent ravines are characterized by large rock outcrops and patches of deep soil. The upper parts of

ravines have relatively more bare rocks and loose stones, and the lower parts more woody vegetation and more ground sparsely covered by grass. *Prunus mahaleb* is often found growing on this kind of mid-elevation rocky or stony slopes in our study area and elsewhere in the Iberian Peninsula. Other abundant woody species are *Crataegus monogyna*, *Quercus ilex*, *Rhamnus alaternus*, *Pistacia terebinthus* and *Rosa* sp. These shrubs or small trees are usually less than 5 m tall (see Gutián et al. (1992), for more information on vegetation cover and height of the Portela site), and most, including *P. mahaleb*, grow mainly in rows along the margins of the stone accumulations. Vegetation is thicker in Portela than in El Estrecho. The riverine woodlands are very narrow (a few meters) stretches of tall *Populus* sp., *Alnus glutinosa*, and *Fraxinus* sp., and shorter *Salix* spp., trees.

We studied fruit removal by birds on samples of the *P. mahaleb* trees in one ravine in Portela (P1) and four adjacent ravines in El Estrecho (E2, E3, E4 and E5). We estimated the frequency of bird species eating *P. mahaleb* fruits by directly watching individual trees. For us, a fruit removal record consisted of a bird grabbing a fruit in the beak; if a bird ate three fruits at a single visit to a tree, we would annotate three fruit removal records. We classified a bird as a “seed disperser” when it carried seeds away from trees, either in the beak or in the gut. Each tree was observed for at least 4 hours (mostly 9–42) distributed throughout different hours of the day, but mostly in the early morning, and during the whole period of ripe fruit availability (May and June). There was no obvious temporal (through the fruiting season) variation in the patterns that we report below. The number of trees sampled in each plot ranged from 11 (E3) to 17 (P1). For analyses of the proportion of fruits eaten by each bird species we excluded trees with less than 10 fruit-removal visits (Tables 1 and 3). We excluded plot E4 because we did not get a sufficient number of fruit-removal records. We made observations in 1992 in plots P1 and E3, 1993 in E5, and 1995 in E2.

Among the vast number of environmental variables that could potentially be correlated with bird visitation to trees, we chose to measure the distance of each tree to the nearest nest of *Phoenicurus ochruros*, a major consumer of *P. mahaleb* fruits in the area whose breeding season lasts until June. We expected that *P. ochruros* would feed more often close to their nests, and that, as a consequence, there would be a negative relationship between distance from a nest and the contribution of this species to the frugivore

Table 1. Percent of fruits taken by each bird species in the four plots (mean across trees; numbers of trees used are shown in brackets).

	P1 (16)	E2 (15)	E3 (11)	E5 (11)
<i>Turdus merula</i>	13.1	55.1	61.4	67.4
<i>Phoenicurus ochruros</i>	42.2	29.5	26.8	32.4
<i>Sylvia atricapilla</i>	41.8	7.0	7.2	0.2
<i>Sylvia cantillans</i>	–	7.2	2.8	–
<i>Parus caeruleus</i>	1.7	–	1.4	–
<i>Erithacus rubecula</i>	1.1	–	–	–
<i>Turdus viscivorus</i>	–	1.2	–	–
<i>Parus major</i>	0.1	–	–	–
<i>Turdus philomelos</i>	–	–	0.4	–
Fruit-removal records	544	283	380	386

assemblage of individual trees. We systematically searched our sites for its nests. They were located inside holes in rock walls. We found one at the top of each of the ravines, plus another one that was in an “outlier” cave situated close to the riverine woodland in El Estrecho, and which was excluded from the study. Thus, each of our plots (P1, E2, E3, E4 and E5) included a single *P. ochruros* nest and a ravine with its associated rows of *P. mahaleb* trees. As all nests were located at one end of a gradient of substrate and vegetation characteristics, this variable is also correlated to habitat characteristics that influence bird activity.

During tree watches, we also annotated the microhabitat type where a bird first perched after feeding on the fruits of *P. mahaleb*. We established four types of microhabitat: (1) rock (bare rock outcrops, usually of several square meters), (2) stones (loose stones on soil), (3) bare or grassy soil, sometimes with scattered low shrubs, and (4) woody vegetation (shrubs, treelets, and riverine woodland). Differences in substrate use between bird species have been used as a measure of the probability of depositing seeds in different microhabitats (Schupp 1993; Jordano and Schupp 2000).

We were interested in the variation of the frugivore assemblage with distance to nests of *P. ochruros*. However, trees within plots are spatially autocorrelated. In other words, they are probably not independent for the purpose of this study and their number should not be used for determining the degrees of freedom of statistical tests. The proper test is to examine whether the expected relationships hold for different plots. Bearing these caveats in mind, and for the sole purpose of showing the direction and quali-

tative strength of the relationships, we calculated correlations for each plot using trees as data points. If these correlations turn out to be generally strong and in the predicted direction in all plots we will reject the corresponding null hypotheses.

Results

Variation of the frugivore assemblage

We recorded nine bird species eating the fruits of *P. mahaleb* (Table 1). Three of them, *Turdus merula*, *Phoenicurus ochruros* and *Sylvia atricapilla*, together comprise more than 90% of the fruit removal records (Table 1). The relative contribution of each bird species to fruit removal (as defined in Methods) varied between the two *P. mahaleb* plots (P1 and E3) studied in the same year, with *S. atricapilla* being quantitatively important only in Portela (plot P1), *Turdus merula* only in El Estrecho (plot E3), and *P. ochruros* in both. There were also minor differences in the frugivore assemblage among the three plots of El Estrecho, which could be attributed to temporal variation, spatial variation, or both.

The total number of fruits removed by the entire set of birds per unit time of observation did not vary with the distance of trees to *P. ochruros* nests (Table 2). However, there were important differences among bird species. In all four plots, the number of fruits taken by *P. ochruros* per unit time of observation was greater on trees closer to their nests. In plot P1 the number of fruits removed by *S. atricapilla* increased with distance to *P. ochruros* nests. The number of fruits removed by *T. merula* was correlated with distance to *P. ochruros* nests in plot E2 only.

We also computed the correlations between the distance of trees to *P. ochruros* nests and the proportional contribution of each bird species to fruit removal (Gutián et al. 1992; Jordano 1994), instead of the absolute number of fruits taken per watching time. The relative contribution of *P. ochruros* decreased with distance to its nests, while those of the other major consumer in each respective plot increased (Figure 1, Table 3). For the two plots (P1 and E2) where these patterns are most significant, the proportional similarity (Renkonen’s index; Jordano (1994); Fuentes (1995)) of frugivore assemblages between pairs of individual trees was negatively correlated to the difference in distance from the two trees to the nearest *P. ochruros* nest (Table 3). As trees are located

Table 2. Spearman rank correlations (two-tailed probabilities in brackets) between distance to nearest nest of *P. ochruros* and the number of fruits taken by birds per tree per hour of observation. Results are presented for all species combined (all birds) and for the three most important species quantitatively. Sample sizes (numbers of trees) for each plot are shown in parentheses. Significant results ($p < 0.05$) are shown in bold type. In the text we discuss important statistical issues related to these analyses.

	Plot			
	P1 (17)	E2 (15)	E3 (11)	E5 (13)
<i>Turdus merula</i>	0.40(0.12)	0.80(0.00)	0.14(0.68)	0.31(0.30)
<i>Phoenicurus ochruros</i>	-0.67(0.00)	-0.84(0.00)	-0.72(0.02)	-0.62(0.03)
<i>Sylvia atricapilla</i>	0.57(0.02)	-0.02(0.93)	0.19(0.57)	0.16(0.77)
All birds	0.24(0.35)	0.41(0.12)	-0.17(0.61)	0.18(0.56)

Table 3. Spearman rank correlations (two-tailed probabilities in brackets) between distance to nearest nest of *P. ochruros* and the proportion of fruits taken by each bird species relative to the total taken by birds. Also shown are the mean proportional similarities (PS, which range from 0 to 1) of frugivore assemblages of pairs of individual trees, and the correlations between PS and the difference between their respective distances to nests. The one-tailed probabilities for these correlations were computed by means of 10 000 Mantel permutations of the data matrices (Fuentes 1995; Jordano 1995). Sample sizes (numbers of trees) for each plot are shown in parentheses. Significant results ($p < 0.05$) are shown in bold type. In the text we discuss important statistical issues related to these analyses.

	Plot			
	P1 (16)	E2 (15)	E3 (11)	E5 (11)
<i>Turdus merula</i>	0.38(0.15)	0.82(0.00)	0.55(0.08)	0.50(0.12)
<i>Phoenicurus ochruros</i>	-0.71(0.00)	-0.85(0.00)	-0.66(0.03)	-0.49(0.12)
<i>Sylvia atricapilla</i>	0.75(0.00)	-0.09(0.74)	0.36(0.27)	0.20(0.55)
Mean PS	0.51	0.50	0.63	0.67
PS	-0.41(0.00)	-0.48(0.00)	-0.22(0.16)	-0.10(0.19)

in rows running down along ravines, and nests are at the top of ravines, this difference is also clearly related to the distance between trees, which we did not measure. In other words, trees at the top of ravines had similar frugivore assemblages, trees at the bottom of ravines had similar frugivore assemblages, and the assemblages at the top were different from the assemblages at the bottom.

Let us emphasize that the important point in these statistical analyses is the fact that the same trends (more fruit-removal records by *P. ochruros*, and less or not different by the other major frugivores, on trees located closer to *P. ochruros* nests) apply to all of our plots, not the specific p values for each particular plot, which are suspect.

Substrate use by birds

We obtained 529 records of substrate use for *P. ochruros*, 383 for *T. merula*, and 160 for *S. atricapilla*. *Phoenicurus ochruros* mainly visited rock, *S. atricapilla* usually flew into woody vegetation, while *T. merula* more evenly visited rock, woody vegetation, stones, and bare or grassy soil (Figure 2). The differ-

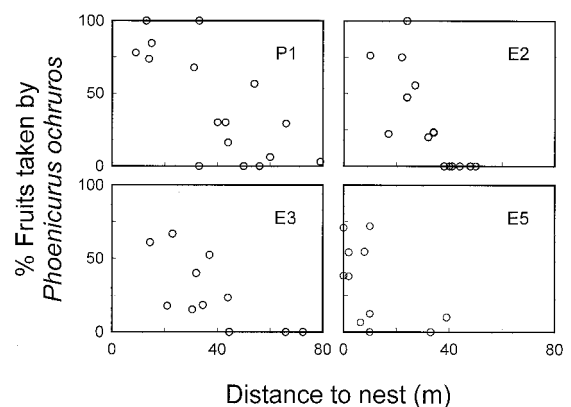


Figure 1. Relationship between percent contribution of *P. ochruros* to avian fruit removal of each tree and distance of trees to *P. ochruros* nests. The results for each plot are graphed separately.

ences among species are statistically significant (chi-square = 627.4, $p \ll 0.001$).

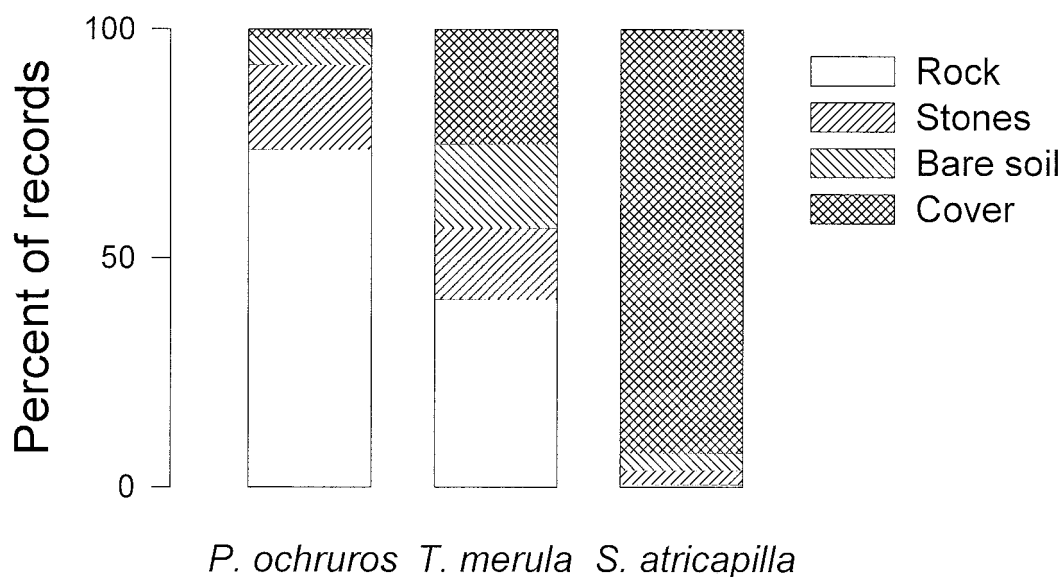


Figure 2. Frequency of substrate use by the three main fruit consumers after feeding on *Prunus mahaleb*.

Discussion

We have found large variation in the avian frugivore assemblage of individual *P. mahaleb* trees in all four plots studied. Fruit removal by *P. ochruros* was highest on trees located closer to their nests in the four plots, while fruit removal by the two other major frugivores (*T. merula* and *S. atricapilla*) was highest away from *P. ochruros* nests in two plots. This variation was probably related to both the location of nests and associated microhabitat characteristics. Adults and fledgelings of *P. ochruros* not only fed heavily on *P. mahaleb* fruits, but also carried large numbers of fruits to feed the nestlings. Territorial aggression towards conspecifics was frequent, and thus the vast majority of observations of *P. ochruros* taking fruits in each plot were of the respective nest owners and their offspring. That *P. ochruros* foraged more often on the trees that were closer to their nests could be due both to the costs associated with travel to and from more distant trees, and to the more favorable microhabitat characteristics in the vicinity of nests, as these were located in areas with a larger proportion of bare rock, a typical foraging substrate of this species (Cramp 1988). We never observed territorial behavior directed towards heterospecific birds; thus, there is no evidence that interference is the reason for reduced visitation by the other bird species to trees near *P. ochruros* nests. Rather, this was probably associated with habitat characteristics. When foraging on foods other than fruits, *Sylvia at-*

ricapilla gleans the foliage of trees and shrubs (Cramp 1992), and *T. merula* picks up invertebrates from the ground, frequently among litter, on a great variety of habitats (Cramp 1988). These substrates were relatively more common away from *P. ochruros* nests.

Variation in the avian consumers of *P. mahaleb* fruits occurs at several scales and due to different causes. This study shows that differences among bird species in their responses to small-scale microhabitat patchiness produce variation in fruit consumers among individual trees within populations. Jordano (1994) found interannual variation in fruit consumers due to changes in the abundance of birds. We cannot address among-year variation with our data because we studied each of our plots during a single season. Differences in habitat structure result in contrasting sets of avian consumers among *P. mahaleb* populations growing only a few kilometers away (Gutián et al. (1992), present study; see also Schupp (1993); Jordano (1994)). In addition, there are significant differences in frugivore assemblages between northwestern and southeastern Spanish populations of *P. mahaleb* (distant 600 km) growing on similar rocky/stony habitats. These are due in part to differences in the regional and landscape-level bird species pools (Jordano 1994). Jordano (1994) argued that the similarity of fruit consumers between plots increased with their geographical proximity. The present study lends support to this idea by extending it to a smaller scale. First, trees located at similar distances to *P. ochruros*

nests tended to have more similar fruit consumers, a relationship that was statistically significant for two of our plots. Second, the average proportional similarity among trees in the present study was 0.58 (Table 3), which is greater than the 0.23 (range 0.20–0.26) average similarity among three local populations in northwestern Spain (Gutián et al. 1992) and 0.49 (range 0.30–0.76) among three local populations in southeastern Spain (Jordano 1994), and the 0.27 (range 0.16–0.18) average inter-regional similarity among the populations from both Spanish areas.

The heterogeneity in the frugivore assemblage is not trivial from the point of view of the plants. We found that the main fruit consumers in our study plots differed markedly in the kinds of microhabitats they visited after foraging on *P. mahaleb*. *Phoenicurus ochrurus* visited bare rock much more frequently than *T. merula* and *S. atricapilla*, and the latter visited woody vegetation more often (for similar results obtained with comparable methods see Herrera and Jordano (1981); Schupp (1993); Jordano and Schupp (2000)). Thus, each of these bird species presumably deposited seeds in different proportions in the different microhabitat types (Hoppes 1987; Reid 1989; Izhaki et al. 1991; Schupp 1993; Chavez-Ramirez and Slack 1994; Larson 1996; Jordano and Schupp 2000). In highly heterogeneous habitats like the ones studied by us, the patch type where a seed arrives may critically affect its chances of becoming an adult tree (Herrera et al. 1994; Schupp and Fuentes 1995). Thus, the identity of the bird species that eat the fruits of a given tree may be an important factor in the fitness of that tree. Fitness differences among genotypes may lead to evolution of fruit traits, but in our case fitness differences mediated by bird visitation patterns may simply arise from the environmental situation of the plants (Thompson and Willson 1978; Moore and Willson 1982; Manasse and Howe 1983; Piper 1986; Denslow 1987; Sargent 1990).

The three main seed dispersing birds in our study showed different patterns of *P. mahaleb* visitation and post-foraging movements within and between microhabitat types. *Phoenicurus ochrurus* mainly takes seeds from trees living at rock outcrops, and tends to deliver them also at rock outcrops. *Sylvia atricapilla* eats fruits on trees surrounded by woody vegetation and probably deposits the seeds also beneath woody vegetation. However, *T. merula* takes seeds mainly from trees surrounded by woody vegetation but tends to deposit them in a variety of microhabitats. Thus, the three species of birds may have different roles in

the patterns of gene flow and neighbor genetic relatedness of *P. mahaleb* within and across habitat patches in the landscape, a question that deserves future research (Sork et al. 1999).

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