Ecological Monographs, 51(2), 1981, pp. 203–218

PRUNUS MAHALEB AND BIRDS: THE HIGH-EFFICIENCY SEED DISPERSAL SYSTEM OF A TEMPERATE FRUITING TREE[1]

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Abstract. Seed dispersal of *Prunus mahaleb* (Rosaceae), a tree producing large fruit crops, was studied in southeastern Spain to establish the degree of reciprocal dependence between the plant and the birds which disperse it. *P. mahaleb* drupes contain a relatively large seed (pulp:stone ratio 0.62). The water content of pulp is 82.9% and dry flesh contains 3.2% crude fat and 2.8% crude protein, being largely made up of carbohydrates. Four bird species were the main seed dispersers. Visitation rates, feeding efficiency, and degree of dependence on *P. mahaleb* fruits for food varied substantially among species. *Turdus merula* and *Sylvia atricapilla* showed the highest visitation rates, were behaviorally the most efficient, removed the bulk of seeds and, after feeding, tended to fly preferentially towards the apparently safest sites for growth and survival of saplings. They were also most heavily dependent on *P. mahaleb* fruits for food, whereas the other disperser species relied largely on insects. Individual plant location and dispersers' habitat preferences produced a differential seeding pattern over the patchy habitat surrounding study trees. The "key" dispersers *T. merula* and *S. atricapilla* are specialized frugivores, efficiently dispersing seeds of a plant producing large numbers of extremely low-reward fruits. These results conflict with theoretical expectations and suggest that both the nature of the correlation between bird- and plant-related coevolutionary gradients and their amplitudes, as well as the nature of bird-plant coevolutionary interactions, may differ between tropical and temperate habitats.

Key words: feeding efficiency; plant-bird coevolution; Prunus mahaleb; *seed dispersal; Spain;* Sylvia atricapilla; Turdus merula.

INTRODUCTION

Seed dispersal may be considered as any nonpassive process by means of which seeds move away from the parent plant to a site suitable for growth and reproduction (Janzen 1975, Howe and Estabrook 1977). Dispersal may facilitate escape from predators (Janzen 1970, 1972), colonization of new habitat patches (Livingston 1972, Smith 1975), and/or gene flow (Levin and Kerster 1974), and it may occur through a great variety of mechanisms (van der Pijl 1972). Vertebrate animals are important dispersal agents and, among them, birds are perhaps most commonly associated with seed dispersal (van der Pijl 1972). Apart from those dispersal systems in which birds are simultaneously dispersers and predators of seeds (Janzen 1971*a*, Vander Wall and Balda 1977, Bossema 1979), the production by plants of "fruits" (any package containing nutritious material plus seeds) and the frugivorous habits of many birds (Lein 1972, Morse 1975) form the basis of the vast majority of plant-bird coevolved systems (Snow 1971, McKey 1975). Furthermore, dispersal of seeds by birds is probably responsible to a large extent for the widespread dominance of angiosperms over much of earth's surface (Regal 1977).

At a community level, the plant-disperser interaction may be represented by a matrix in which rows are plant and columns are bird species. Cells may contain any measure of the degree of interaction between plant and disperser. Selecting a row in the matrix and studying interdisperser differences in their effects on the plant has been the usual approach in recent years (McDiarmid et al. 1977, Howe 1977, Howe and Steven 1979, Howe and Vande Kerckhove 1979, Jordano 1979). These "row" studies provide a view of the dispersal system from the plant's viewpoint, and inform us about disperser traits enhancing efficient dispersal of the plant species concerned. Selecting a column in the matrix and studying interplant differences in their effects (feeding value) on the disperser species has been a more traditional approach (e.g., Hartley 1954, Snow 1962*a*, *b*, *c*, Snow and Snow 1971), although results have not always been interpreted in the light of current coevolutionary models. "Column" studies provide the disperser's view of the system, and they can inform us about plant traits which enhance utilization by dispersers.

Analyzing the entire matrix, or some sufficiently large subset, is the only way to test the predicted interactions between plant- and disperser-related coevolutionary gradients (McKey 1975, Howe and Estabrook 1977). We know of no temperate work, and only a few tropical examples, in which information of this kind has been provided (Crome 1975, 1978, Trejo 1976, Kantak 1979, Stiles 1979, Frost, *in press*), although usually the importance of nonfruit food to the various

[1] Manuscript received 9 April 1980; accepted 3 October 1980.

disperser species has not been quantified and/or results have not been interpreted on a coevolutionary basis. In tropical habitats, where most recent studies on plant-frugivore interactions have been carried out, very high species diversities of both plants and dispersers largely prevent studies of this kind. Temperate habitats provide much simpler study systems and, as in the present study, situations in which a single plant species is fruiting at a given time in a habitat are not rare, providing a special case for a "matrix" study. Temperate studies are also needed as comparisons with analyses from tropical systems, from which recent theory has mostly developed (Snow 1965, Smythe 1970, Morton 1973, McKey 1975, Howe and Estabrook 1977). Although some studies dealing with plant-bird coevolutionary relationships in temperate habitats have recently appeared (Salomonson and Balda 1977, Thompson and Willson 1978, 1979, Herrera 1981), they continue to be underrepresented with respect to tropical ones. We present in this paper the results of an investigation of the dispersal of *Prunus mahaleb* L. (Rosaceae) by birds, and the degree of reciprocal dependence between the plant and its seed dispersers.

Study Site

Field work reported in this paper was mostly carried out from 14 to 18 July 1979 at a group of five *P. mahaleb* trees growing close to the Casa Forestal de Roblehondo (37°56′N, 2°52′W, 1300 m elevation), in the Sierra de Cazorla, Jaén province (eastern Andalusia, Spain). Descriptions of the Sierra de Cazorla, a rough mountain range extending over 40 km (maximum elevation 2107 m), can be found in Fernández-Galiano and Heywood (1960), Polunin and Smythies (1973:83–89), and Otero et al. (1978). Data were mainly collected at the three trees bearing the largest fruit crops, but casual observations were also made on the other two. The five trees were located within a circle of 50-m radius, on a dry, rocky, north-facing slope, in a partially cleared area around the Casa Forestal. They grew in a readily discernible mosaic of vegetation types, with patches differing mainly in vegetational composition and vertical complexity. Tall pines at varying densities (*Pinus nigra*), variously sized patches of deciduous thorny shrubs (*Berberis hispanica, Crataegus monogyna, Prunus spinosa, Rosa* spp., and *Rubus ulmifolius*), and areas covered by broad-leaved evergreen trees (mainly *Quercus ilex* and *Phillyrea latifolia*), were the principal vegetational components of the mosaic surrounding the study trees. The site was located on a transtitional zone between mediterranean sclerophyllous (*Q. ilex–P. latifolia*) and montane (*Pinus nigra–B. hispanica*) vegetational formations.

Mean annual rainfall at the closest meterological station (Santiago de la Espada, 15 km to the northeast, 1328-m elevation) is 673 mm. Mean annual temperature is 12.3°C, the highest occurring in July (23.2°C), the lowest in January (3.3°C) (Montero and González 1974). Snowfalls are frequent from November to March, but snow usually remains for <1 wk.

Complementary observations were conducted at two groups of *Prunus mahaleb* trees growing elsewhere in the Sierra de Cazorla. They were located in the Cañada de las Fuentes (15 km southwest of Roblehondo, 1400-m elevation) and Solana de Cagasebo (19 km south-southwest of Roblehondo, 1650-m elevation).

Methods

Height and horizontal crown projection of the trees were measured, and the size of their standing fruit crops estimated. To calculate the total number of fruits produced over the entire fruiting period and assess the phenological stage, the numbers of ripe, unripe, and missing fruits were counted on a sample of branches (N = 12–26) from each tree. The position of the trees was plotted on a map and the structure of the habitat around the main study trees was assessed by measuring the length occupied by each of seven qualitative, structural habitat components along 20 evenly spaced, 100 m long radial transects departing from the tree. Habitat components considered were open rocky ground, open grassy ground, low shrubs (<1 m), high shrubs (1–3 m), broad-leaved trees (>3 m), sparse pines (nearest neighbor distances > 25 m), and dense pines (distances <25 m).

To estimate the quantity of ripe fruits falling to the ground beneath the trees, and the relative magnitude of consumption by mammals at night and deterioration in situ, counts of fallen fruits were carried out under trees 3 and 5 at dawn and dusk from the evening of 14 to the morning of 18 July. Between 11 and 15 quadrats (30 cm × 30 cm) were regularly placed on the ground along a line lying just below the outer third of the crown, and all fruits found within the quadrats were counted. At tree 3, 12 piles (20 fruits each) containing either desiccated or fresh fruits, or a 1:1 mixture of both types, were randomly placed on the ground beneath the crown to assess the rate of deterioration and consumption of fallen fruits, and to complement the information obtained from quadrat counts. Daily counts at the piles were also carried out at dawn and dusk.

A sample of ripe fruits was collected from trees 3 and 5 to prepare pulp samples for chemical analyses and to obtain fruit masses and measurements. Observations of the qualitative nature of the distribution of *P. mahaleb* saplings were conducted on the area surrounding the trees on July study dates and during 4–9 August.

Observations of birds were made almost continuously from dawn to dusk from 15 to 17 July. At any

given tree, 1-h observation periods were distributed as evenly as possible over daylight. Trees 3 and 4 were observed simultaneously owing to their closeness, and periods of observation at these trees were alternated with those at tree 5. One-hour observation periods were usually separated by 1–2 h at each tree.

Two kinds of observations were carried out. One of us (P. Jordano) recorded the identity of all birds entering and leaving the tree. The landscape around each tree was divided into six sectors according to easily recognizable, prominent features, and the origin of birds entering the tree and the flight directions of those leaving it were assigned to the corresponding sector whenever possible. The second observer (C. Herrera) carried out observations on feeding behavior of individual birds at the fruiting trees. Whenever possible, the following data were recorded: (1) total time spent by the bird at the tree, (2) number of fruits ingested, (3) number of times a bird moved within the tree crown while engaged in fruit feeding. Birds could not always be observed during their entire stay in the tree ("total" observations hereafter), and in these instances data on (2) and (3) above were taken and scaled according to the total time the bird was under observation ("partial" observations). Unsuccessful fruit-feeding attempts and behavior utilized to ingest fruits were also recorded when possible. All behavioral interactions between birds at the trees, and avian predators seen in the area in the course of our observations, were noted as well.

Three mist-nets were employed on 4 d during short time intervals irregularly distributed during the day. Nets were situated 10–50 m from the closest *P. mahaleb* tree. All birds caught were weighed, ringed, and released. Fecal samples were obtained by flushing the digestive tract with 1% sodium chloride water solution (Moody 1970, Brensing 1977). Feces were collected on filter paper and air dried immediately for storage. Prior to analysis, they were wetted for 24 h. Each sample was examined individually and the remains were sorted. The percentage made up by insect and fruit remains other than seeds (usually fruit skins) was estimated visually to the nearest 10%. Hertwig's solution (Baumgartner and Martin 1939) was added to fruit skins on a microscope slide, which was heated briefly on a flame, and examined under a microscope at 125 magnifications. Identification was accomplished by comparison of size and shape of cells with an extensive reference collection of fruit skin microphotographs. The minimum number of fruits represented in every individual fecal sample was estimated from the number of seeds (when present) and the amount of fruit skin present, and the largest figure was taken as representative for the sample.

Mist-nets were used again from 6 to 10 August at the same locations, after the crops of *P. mahaleb* trees had been completely exhausted, to obtain comparative data on bird abundance.

The Trees

Prunus mahaleb is a small deciduous tree distributed throughout central and southern Europe, northwestern Africa, and west-central Asia (Webb 1968, Ceballos and Ruiz 1971). In Spain, the species has been reported as favoring relatively mesic sites in cool-temperate climate areas (Ceballos and Ruiz 1971), and in the southern half of the Iberian Peninsula it is only found as local populations in mountains. The population of Sierra de Cazorla lies on the southwestern boundary of its European range. Isolated individuals or small groups of sparse *P. mahaleb* are found there scattered at elevations between 1200 and 1800 m, wherever natural vegetation has not been too seriously disturbed in recent decades by establishment of pine plantations. It is found growing on shallow, rather poor soils from thickets in the vicinity of streams to dry hillsides.

Of the 11 woody plant species producing fleshy fruits in Roblehondo, *P. mahaleb* is the earliest to bear ripe fruits, and the only one that did during the study dates. In 1979 flowering took place in early May, by mid-June unripe fruits were about full size, and ripening began in late June or early July. By early August, not a single fruit could be found either on the trees or the ground beneath them. Ripening periods of trees at Cañada de las Fuentes and Solana de Cagasebo, at higher elevations, differed substantially, for they still had virtually intact fruit crops on 4 August. On this date, trees at these localities had matured $<10\%$ of their total crops.

Ripe drupes are bright black, 8.0 ± 0.4 ($\bar{x} \pm 1$ SD) mm long and 8.3 ± 0.5 mm wide ($N = 20$), and are held in axillary clusters of one to six fruits. Fresh mass of individual drupes is 0.38 ± 0.05 g ($N = 20$), and that of the one-seeded stone is 0.10 ± 0.02 g ($N = 5$). Fresh mass of pulp per drupe is 0.27 ± 0.05 g ($N = 5$) and its water content is as high as 82.9%. An average drupe has only 0.05 ± 0.01 g ($N = 20$) of pulp, as compared to 0.08 ± 0.01 g ($N = 25$) of dry stone (pulp:stone ratio = 0.62). Chemical analyses of dry pulp yielded 3.2% crude fat, 2.8% crude protein, 6.3% ash, and 5.7% fiber. "Soluble" carbohydrates amount to 82.0% (obtained by difference), thus the pulp of *P. mahaleb* in fresh state may be seen as a sugary water containing trace amounts of fat and protein.

The number of ripe fruits per tree on the study dates varied from <1000 up to 20 000 (Table 1). As estimated from branch counts, the phenological stage varied slightly among trees, although all were at or close to the middle of their fruiting period. Total crops produced over the entire 1-mo fruiting period can be estimated from the figures on standing crops and the percentages of ripe fruits derived from branch counts. Projected total crops show large differences among trees, which must be related to both tree size and degree of shading by overtopping vegetation. Trees re-

TABLE 1. Tree and crop sizes, and phenological stages of five *Prunus mahaleb* trees at Roblehondo, 15–18 July 1979.

Tree number	Height (m)	Crown projection (m^2)	Standing ripe fruits	Estimated total crop	Branch counts (% of fruits)			
					Ripe	Unripe	Missing	*N*
1	3.0	7.8	150	2400	6.3	25.3	68.4	79
2	3.5	12.8	350	2400	14.8	61.3	23.9	142
3	4.5	45.4	20 000	80 000	25.0	23.3	51.7	240
4	2.5	9.2	900	3500	26.0	5.8	68.2	346
5	4.5	33.7	8000	25 000	32.0	33.1	34.9	587

ceiving the most insolation (numbers 3 and 5) bore the largest crops and were also the largest trees, but they produced crops disproportionately large for their size in comparison with the remaining three. The extraordinary crop of tree 3 had a fresh mass of ≈30 kg produced over the entire fruiting season, with nearly 8 kg standing on the tree on study dates. This does not appear to be unusual for *P. mahaleb*, for similar crop sizes have been observed frequently elsewhere in the Sierra de Cazorla.

Besides the group of trees studied, a few other trees with fruit were found scattered within 1 km of our study site. Nonreproductive individuals of varying sizes were frequent, mainly as small saplings <0.5 m high. These were mostly found under bushes, among rocks, or under dense holly-oak (*Q. ilex*) undergrowth, often >30 m from the nearest reproducing tree. This indicates that reproduction from seeds is occurring in the area. Not a single sapling was found in the open, whereas a few dozen were recorded under cover or among rocks despite the greater difficulty involved in surveying these sites. The heavy grazing pressure in the area by wild ungulates, mainly fallow deer (*Dama dama*), but also Spanish wild goats (*Capra pyrenaica*) and red deer (*Cervus elaphus*), coupled with a distinct pattern of seed dispersal (see below), are most likely responsible for this pattern of sapling distribution.

THE BIRDS

Fruit-eating species

Six bird species were seen ingesting whole fruits (Table 2) at *Prunus mahaleb* trees. Two of these will not be considered here; *Garrulus glandarius* was extremely rare and *Erithacus rubecula* (not listed in Table 2) was seen feeding at tree 3 only outside observation periods. *Turdus merula* and *Sylvia atricapilla*, the most frequent visitors at all trees, together made up 71.8% of all visits recorded. Visits by the two *Phoenicurus* species, although significant, were much less frequent at trees 3 and 4, whereas at tree 5 they constituted 44.2% of visits. Observations at *P. mahaleb* fruiting trees growing in Cañada de las Fuentes and Solana de Cagasebo revealed that *T. merula*, *S. atricapilla*, and *Phoenicurus ochruros* were also regular visitors there. This suggests a significant constancy in the species of birds eating *P. mahaleb* fruits, irrespective of elevation, date, and phenological stage.

Apart from the 987 visits of fruit-eating birds presented in Table 2, a very small number of visits by five other passerine species was recorded in the same observation intervals (number of times in parentheses): *Parus caeruleus* (4), *Emberiza cia* (2), *Fringilla coelebs* (2), *Emberiza cirlus* (1), and *Parus ater* (1). Except for *P. caeruleus*, which occasionally pecked at the pericarp of a few fruits, the remaining four species did not pay any attention to fruits while in the trees.

Besides the above-mentioned species, individuals of five others were captured in mist-nets and/or were seen foraging in the area (*Regulus ignicapillus, Phylloscopus bonelli, Parus cristatus, Troglodytes troglodytes, Loxia curvirostra*), totalling 16 passerine species recorded in Roblehondo during our visit. Disregarding four species which strongly specialize in ground seed eating (*Emberiza* spp., *F. coelebs*) or cone opening (*L. curvirostra*), a marked pattern exists which relates mean body mass to *Prunus mahaleb* fruit consumption. All species which did not eat fruits are <12 g, while those which did are >14 g, with no overlap between the ranges of the two species groups (Fig. 1A). There exists a significant correlation between log body mass and bill width ($r = .954$, $n = 12$, $P < .001$). Bill width ranges are 4.7–12.1 mm and 2.9–3.6 mm for species eating and not eating *P. mahaleb* fruits, respectively.

TABLE 2. Visits of fruit-eating birds recorded at the *Prunus mahaleb* study trees during regular observation periods. *N* = total number of visits recorded.

Bird species	Percent of visits			
	Tree 3 (*N* = 400)	Tree 4 (*N* = 146)	Tree 5 (*N* = 441)	All combined (*N* = 987)
Garrulus glandarius	0.5	...	...	0.2
Turdus merula	25.3	41.1	23.6	26.8
Sylvia atricapilla	58.8	45.8	32.2	45.0
Phoenicurus ochruros	5.7	2.1	23.1	13.0
Phoenicurus phoenicurus	9.7	11.0	21.1	15.0
Observation time (h)	13.5	13.5	9.8	36.8
Overall visitation rate (visits/h)	29.6	10.8	45.4	26.9

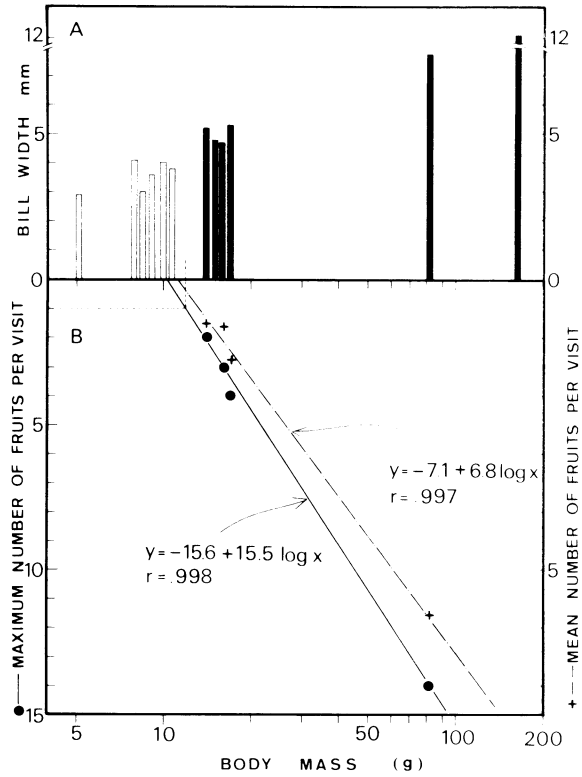

FIG. 1. A. Body mass and bill width of passerine species eating (solid bars) and not eating (open bars) *P. mahaleb* fruits in the Roblehondo study site. Four species showing extreme morphological adaptations (to cone opening and ground seed eating) have been omitted (see text). B. Regression of body mass on mean (broken line) and maximum (solid line) number of fruits ingested per visit. See text for further details.

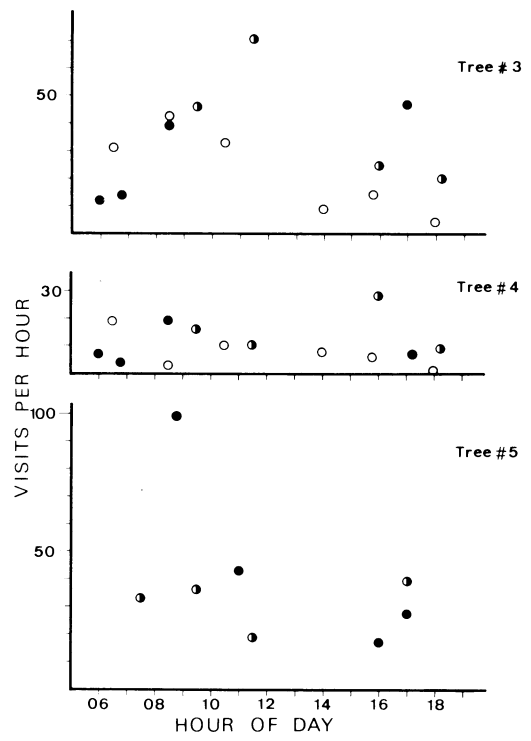

FIG. 2. Actual hourly visitation rates (all fruit-eating bird species combined) recorded at three *P. mahaleb* study trees on days 15, 16, and 17 July 1979 (open, filled, and half-filled circles, respectively).

Visitation rates

Overall visitation rates varied widely among trees (Table 2), from 10.8 to 45.4 visits/h, with considerable daily and hourly variation also occurring within any tree (Fig. 2). Actual hourly visitation rates varied between 4 and 71 (tree 3), 1 and 28 (tree 4), and 17 and 98 (tree 5) visits/h, thus encompassing a hundredfold difference. The highest mean rate recorded was 1 visit/36 s. Rates at tree 4, which had a small crop, were mostly <20 visits/h, while rates at the other two, with much larger crops, were usually above that figure. Casual observations at trees 1 and 2, which bore crops comparable to tree 4, suggested that their visitation rates were at least one order of magnitude less than those recorded at the latter. Tree 4 may have benefited from its proximity to the largest tree, number 3.

Although a trend towards higher visitation rates during the morning appears to be shared by all trees, considerable variation occurs at any tree and time of day (Fig. 2). This fact, together with the widely overlapping ranges of visitation rates between trees and a poorly defined diurnal cycle, all make the number of birds present at any given time and tree fairly unpredictable.

Feeding behavior

In this and the next section, data from the three trees observed have been combined into a single sample, since preliminary analyses failed to show significant intertree differences in bird behavior.

Two feeding techniques were commonly used by the four principal fruit-eating species. The most frequent was taking fruits while perched close to a fruit cluster. Less frequently, birds took fruits in flight by hovering in front of them. On a few occasions outside regular observation periods, *T. merula* was seen feeding on fallen fruit under tree 5. There are highly significant interspecific differences in the relative frequencies with which each technique is used (Table 3). Whereas *T. merula* and *S. atricapilla* fed almost exclusively while perched, one-third of feeding attempts recorded for the two *Phoenicurus* species were made by hovering. Because hovering is mainly restricted to the periphery of the crown, these differences in feeding behavior also are reflected in differences in the zone of tree used; *Phoenicurus* mainly frequented the outermost layer and the remaining species foraged over the whole crown.

The success of fruit-eating attempts was nearly

TABLE 3. Feeding behavior and success of feeding attempts of the most common fruit eaters. N = number of observations.

Bird species	N	Percent		Percent	
		Hovering	Perched	Successful	Unsuccessful
1. *T. merula*	201	0	100.0	99.5	0.5
2. *S. atricapilla*	113	2.7	97.3	98.2	1.8
3. *P. ochruros*	51	33.3	66.7	52.9	47.1
4. *P. phoenicurus*	42	33.3	66.7	81.0	19.0
Difference species 1 and 2 vs. 3 and 4					
Chi squared (df = 1)		97.7		102.1	
$P <$		.001		.001	

100% in *T. merula* and *S. atricapilla*, and much lower in the two *Phoenicurus* species; differences between the *Phoenicurus* and the other two species combined were highly significant (Table 3). An attempt was considered successful when the bird actually swallowed the fruit. Most failures among *Phoenicurus* derived from an inability to detach a fruit from its peduncle and, less frequently, from dropping it during the few seconds it was held in the bill before swallowing.

T. merula spent the most time at the tree and consumed the greatest number of fruits (Table 4). *S. atricapilla* and the two *Phoenicurus* spent about the same time at the tree, but the former removed nearly twice as many fruits in each visit. Number of fruits eaten per minute ranged from 1.9 (*P. ochruros*) up to 5.5 (*T. merula*). Another parameter relating to the efficiency with which fruits are harvested is the number of times a bird moves (flying and/or hopping) within the tree per feeding attempt, since it represents an estimate of the energetic loss involved in obtaining fruits. Significant interspecific differences exist, with *P. phoenicurus* being the most restless species and *T. merula* the least.

Nearly perfect correlations exist (Fig. 1B) between species log mean body mass and either mean number of fruits consumed per visit ($r = .997$, $n = 4$, $P < .01$) or maximum number recorded in a single visit ($r = .998$, $n = 4$, $P < .01$). The intercept of the equation relating maximum number of fruits per visit and log body mass on the line $y = 1$ occurs for a body mass of 11.7 g, and the intercepts of both equations on the x-axis are 10.1 and 11.3 g. These values fall precisely between the ranges of frugivorous and nonfrugivorous species. Regression equations thus appear to predict accurately, on the basis of observed ingestion rates of the most common frugivores alone, that birds <11 g are unable to feed on *P. mahaleb* fruits.

Behavioral interactions at fruiting trees

A total of 22 interactions was noted during our observations, and generally these consisted of supplanting attacks. Most displacements were executed by *T. merula*, the heaviest-bodied species, and directed mainly towards individuals of other species (Table 5). Relative frequency of displacements of any species was measured by the ratio of number of times displaced to total number of feeding attempts recorded for that species. This does not mean, however, that interactions actually took place in connection with feeding attempts. *P. phoenicurus*, the lightest species,

TABLE 4. Body mass and foraging statistics of the four most common avian fruit eaters at *P. mahaleb* study trees. $\bar{x} \pm$ SD, sample size in parentheses.

	Mean body mass* (g)	Length of visit† (s)	Fruits ingested per minute‡	Fruits ingested per visit† [maximum]	Moves per feeding attempt‡
T. merula	81.2 (18)	69.7 ± 38.2 (42)	5.5 ± 4.0 (44)	5.8 ± 4.4 (24) [14]	1.0 ± 0.7 (21)
S. atricapilla	16.8 (15)	31.8 ± 27.1 (60)	3.7 ± 3.6 (83)	1.4 ± 0.7 (56) [4]	1.6 ± 1.2 (56)
P. ochruros	16.2 (5)	40.4 ± 36.7 (35)	1.9 ± 3.6 (36)	0.8 ± 0.6 (32) [3]	1.9 ± 1.9 (17)
P. phoenicurus	14.1 (9)	31.2 ± 15.7 (34)	3.1 ± 10.2 (36)	0.7 ± 0.5 (30) [2]	2.2 ± 1.9 (20)
F value		15.1	3.1	39.4	2.9
$P <$		.001	.05	.001	.05

* From bird individuals mist-netted in the study locality.
† Computed from "total" observations only.
‡ Computed from both "total" and "partial" observations.

TABLE 5. Summary of aggressive interactions recorded at the fruiting trees.

	Times displaced*	Times displaced per feeding attempt	Excess time† (%)
T. merula (*T.m.*)	2 (*T.m.* 2)	0.010	8.0
S. atricapilla (*S.a.*)	8 (*T.m.* 5, *S.a.* 3)	0.071	30.8
P. ochruros	4 (*T.m.* 1, *S.a.* 1, *P.p.* 2)	0.078	37.0
P. phoenicurus (*P.p.*)	8 (*T.m.* 5, *P.p.* 3)	0.190	52.9

* Displacements performed by those species whose initials appear in parentheses, followed by the number of times displacement by that species occurred.

† Mean visit length minus average time required to ingest an average fruit load at average ingestion rate, expressed as percent of the former. See text for further details.

was displaced on the average once every five feeding attempts and *T. merula,* in the opposite extreme, only once every 100 feeding attempts.

Presumably the occurrence of these interactions represents a waste of time while birds are foraging for fruit, especially to frequently displaced species. Active avoidance of interactions may represent a permanent pressure on foraging birds, with a consequent further decrease in the overall rate of fruit ingestion. By dividing the number of fruits eaten per visit (computed from "total" observations alone) by the number of fruits eaten per minute (computed from "total" and "partial" observations), it is possible to estimate for each species the expected average time required to ingest an average fruit load (fruits per visit in Table 4). Difference between actual and expected values, expressed as percent of the former, will be called "excess time" (Table 5). All four species spent more time at the tree than necessary to collect an average fruit load at average ingestion rate, but excess time differs greatly among them, with *T. merula* spending only 8% more time than necessary and *P. phoenicurus,* on the opposite extreme, 52.9%. The correlation coefficient between excess time and the ratio, displacements:fruit attempts (previously transformed with arcsin) is positive and significant ($r = .980$, $n = 4$, $P < .05$). No significant correlation exists between excess time and the ratio of number of aggressions initiated by a species to total feeding attempts ($r = .040$; arcsin-transformed data). This strongly suggests that frequent aggressive interactions are responsible (directly and/or via active avoidance) for a requirement of longer foraging time at the tree than expected on the basis of bird foraging rates alone, which thus lowers overall fruit ingestion rate. On the other hand, species usually initiating displacements do not impair their foraging rate for this reason.

Dependence on Prunus mahaleb *fruits for food*

The huge fruit crops produced by *P. mahaleb* trees attracted large numbers of individuals of the four main frugivorous species, most of which left the area following complete crop depletion. As estimated by mist-netting yields, local abundance of the main fruit-eating species decreases substantially following the exhaustion of crops at Roblehondo. During 14–18 July, the four species together yielded 58 birds/100 net-h, and represented 72% of all birds trapped. By 6–10 August, yield was only 10 birds/100 net-h, signifying 40% of all individuals netted. The most marked declines were shown by *S. atricapilla* (from 21 to 2 individuals/100 net-h) and *T. merula* (from 23 to 3). Yields of non-frugivorous species varied much less markedly, from 22 to 15 individuals/100 net-h in July and August, respectively. On August netting dates, the only ripe fruits available in Roblehondo were those of several individuals of *Lonicera etrusca* (Caprifoliaceae), a woody climber usually producing not more than a few hundred berries per plant. These were being rapidly depleted by the few *T. merula* individuals still remaining in the area.

From observations at the trees alone it is not possible to assess the degree to which temporary populations of fruit-eating species depend on *P. mahaleb* for subsistence. Individuals of a locally very abundant species who visit the tree infrequently, and have fruit as a minor element in the diet, could give the impression of greater dependence on the tree than a rare species which visits the tree very often and depends almost entirely on fruit for subsistence. The actual feeding value of fruits can only be correctly assessed by determining their proportion in the diets. We obtained this information by analyzing fecal samples from mist-netted birds in the vicinity of *P. mahaleb* trees (Table 6).

Except for a single broken seed of *Rubus* sp. found in a sample from *S. atricapilla,* all fruit remains (both seeds and skins) found in the 57 fecal samples analyzed belonged to *P. mahaleb* drupes. We do not know where the above-mentioned *S. atricapilla* could have ingested the *Rubus* seed, since by the time of our visit these plants were in full bloom, and the first ripe fruits at Roblehondo were found by late August. All samples from *T. merula, S. atricapilla,* and *Phoenicurus ochruros* had *P. mahaleb* remains, demonstrating that the frugivorous habit was fully extended among the individuals of these species. Only 78% of *Phoenicurus phoenicurus* feces examined had fruit remains. All seeds recovered from feces were apparently intact.

TABLE 6. Relative importance of *P. mahaleb* fruit remains in fecal samples of the four most common avian fruit eaters at Roblehondo.

	Number of samples	Percent containing *P. mahaleb*	Percent volume of fruit material*	Minimum fruit number present per sample*†
T. merula	20	100	75 ± 27 (10–100)	2.6 ± 3.1 (0.1–13.0)
S. atricapilla	16	100	78 ± 20 (30–100)	1.4 ± 1.2 (0.1–4.0)
P. ochruros	12	100	50 ± 24 (20–80)	0.2 ± 0.1 (0.1–0.5)
P. phoenicurus	9	78	25 ± 27 (0–70)	0.3 ± 0.3 (0.1–1.0)

* $\bar{x}$ ± 1 SD. Observed range in parentheses.
† Computed using only those samples which contained some fruit remains.

Mean percent of fecal sample volume made up by fruit remains other than seeds is not necessarily an accurate estimate of the relative importance of fruits in the diet, but we believe it is suited for comparative purposes. Sampled individuals of *T. merula* and *S. atricapilla* were those relying most heavily on *Prunus mahaleb* fruits for food, with close to 75% of feces volume made up by fruit remains on the average. Some samples from these two species contained exclusively *P. mahaleb* remains. In decreasing order of fruit significance are *Phoenicurus ochruros* and *P. phoenicurus*, with fruit remains representing ≈50 and 25% of feces volume, respectively. All nonfruit material identified in feces was made of insect remains. The mean number of fruits represented per sample (minimum estimate) is highest in *T. merula* and *S. atricapilla*, and lowest in the two *Phoenicurus* species. All these results demonstrate that the four most common species at *Prunus mahaleb* trees depend to a very variable extent on the consumption of fruits for subsistence.

Predation

Although no actual predation attempt on birds feeding at fruiting trees was observed in the course of our field work, single individuals of the Sparrow Hawk *Accipiter nisus* were seen daily in the area. A bird of this species was seen flying over our study trees carrying a *T. merula* in its feet, and on another occasion a bird was seen actively hunting by suddenly approaching *Rubus* bushes nearby. Sparrow hawks are abundant in all wooded habitats of the Sierra de Cazorla, being observed virtually every day despite their discrete habits; thus it is probably the most important local predator on small passerine species such as those feeding on *Prunus mahaleb* fruits. In addition, we observed *Falco tinnunculus* (two times), *Hieraetus pennatus* (five), and *Buteo buteo* (three) at Roblehondo during the study period, all of them potential predatory species on small birds. Our observations reflect the great abundance and diversity of birds of prey in the Sierra de Cazorla (at least 10 predatory species wihin the Falconiformes can be found in appreciable densities [Otero et al. 1978]), and the important predation pressure on small passerines as compared to that in more disturbed areas.

THE DISPERSAL

How do seeds leave the parent tree?

The four bird species dealt with in the preceding section ingest whole fruits, and defecate (*T. merula* and *S. atricapilla*) or regurgitate (*Phoenicurus* spp.) the seeds in an apparently intact condition; thus the birds must be considered true dispersers of the plant. By combining information on visitation and ingestion rates presented above, the number of seeds removed by each species was estimated on a daily basis. Removal rates were 909, 436, and 1226 seeds/d for trees 3, 4, and 5, respectively. The relative contribution made by each species to these overall figures is shown in Fig. 3. *T. merula* removed the most seeds from the trees (61.4–76.8%), followed by *S. atricapilla* (20.0–33.5%). The two *Phoenicurus* species were responsible for the removal of only 3.3–16.0% of all seeds taken away from the trees by birds. There are slight intertree differences in the importance of *T. merula* and *S. atricapilla* as seed vectors, and much more marked ones in the importance of *Phoenicurus*.

The above figures refer only to seeds actually removed from the tree, but fruits also fall to the ground beneath it, which could constitute a further route for seeds leaving the parent tree. Magnitude of fruit fall over 3 d at trees 3 and 5 was estimated from quadrat counts. Average daily rate estimates of fruit-fall were 256 and 167 fruits, thus representing 21.9 and 12.0% of seeds leaving the branches of the parent tree every day in trees 3 and 5, respectively (Fig. 3). These rates presumably vary according to weather and stage in the fruiting period, so they must be taken as very rough estimates. As revealed by control piles, fallen fruits become desiccated rapidly, usually within 24 h, and ants avidly eat the flesh of newly fallen fruits; thus only a small fraction of all fruits on the ground are in good condition at any given time.

The fate of fallen fruits is difficult to assess quantitatively, since most fruit consumption takes place at night (67.5 and 92.0% of daily consumption of fallen fruits recorded beneath trees 3 and 5, respectively). Diurnal consumption must be attributed to *T. merula*, which was seen on several occasions foraging under the trees. Nocturnal consumers were probably mainly fallow deer, but also to some extent wood mice (*Apo-*

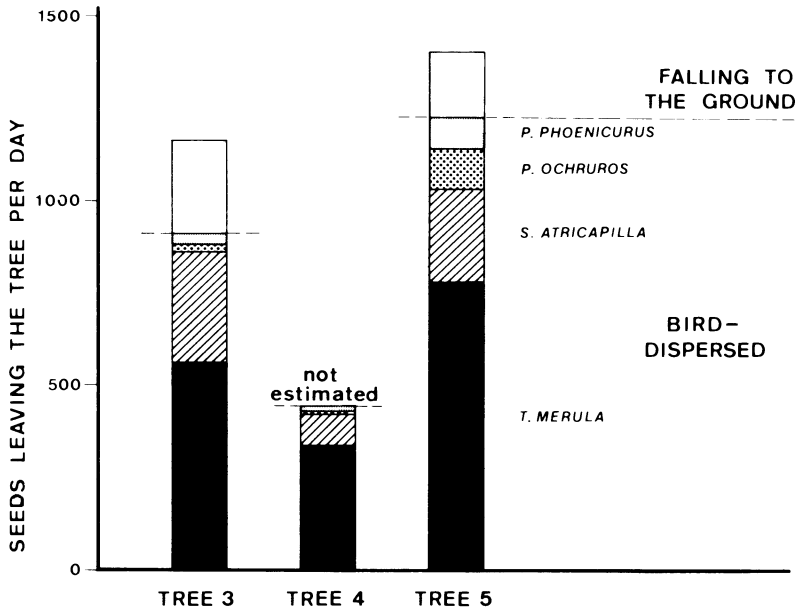

FIG. 3. Estimates of the fate of seeds leaving the branches of *P. mahaleb* study trees every day.

demus sylvaticus) and red fox (*Vulpes vulpes*). Scats of the latter containing many intact *Prunus mahaleb* seeds were found near fruiting trees in Cañada de las Fuentes, thus the red fox may be considered a potential disperser of the plant. This is not so for deer, which seem to destroy all seeds ingested, as determined from the examination of feces collected at Roblehondo. It is not possible at present to assess the relative importance of fruit consumption by nocturnal species, but our impression is that most nighttime fruit feeding in Roblehondo is attributable to deer and, consequently, results in seed destruction.

Available data sugest that the four most common bird visitors are responsible for the removal of at least 78 and 88% (trees 3 and 5, respectively) of seeds leaving the parent tree daily. These figures represent minimum estimates of the proportion of seeds leaving the tree in undamaged condition, since a small fraction of fruits on the ground is secondarily "saved" by *T. merula*. The great majority of the remaining seeds appears to be destroyed by deer and, therefore, the four most common bird visitors perform virtually all the dispersal of *P. mahaleb* at Roblehondo.

Where do seeds go?

Flight directions of birds departing from the tree after fruit feeding are responsible for the distribution of seeds over the habitat surrounding the parent tree. Tendencies to fly to particular locations around the tree will generate heterogeneous seeding patterns, and these may vary according to the disperser species concerned. At our study trees, individuals of each bird species tended to fly preferentially to and from certain habitat sectors around the tree and, for any species, directionality of flights varied among trees as well (Fig. 4).

Simultaneous consideration of arrival flights and the relative position of the trees suggest the existence of interplant interference. A tree tends to receive most visits from those habitat sectors around it which lack other conspecific fruiting plants. Arrivals from west and southwest take place mostly at tree 5, from north at tree 3, and from east, south, and southeast at trees 3 and 4. Mutual interference between trees was very evident in the field, since birds coming to the group of fruiting trees almost invariably landed on the first tree they encountered on their way. Departing and arriving flight patterns are very similar; favored arrival sectors of each tree were the usual routes of departure (Fig. 4). This also holds at an individual level. For the four bird species combined, 49.8% of the 227 individuals for which complete data exist arrived and left the tree by the same flight sector, 29.1% left it on any of the two contiguous ones, and only 21.2% departed through any of the noncontiguous sectors. These results indicate that the overall pattern of departing flights from a given tree, and hence its seed flow, are partially influenced by the presence of other neighboring fruiting trees, through the effect of the latter on arrival patterns and the predominant agreement between arrival and departure directions of individual birds.

Within a given tree, interspecific differences in flight patterns of dispersers cannot be explained in this way, but rather as a consequence of differences in dispersers' habitat preferences. Each flight sector of trees 3 and 5 was characterized by the relative importance (cover) of each of seven habitat components, and cor-

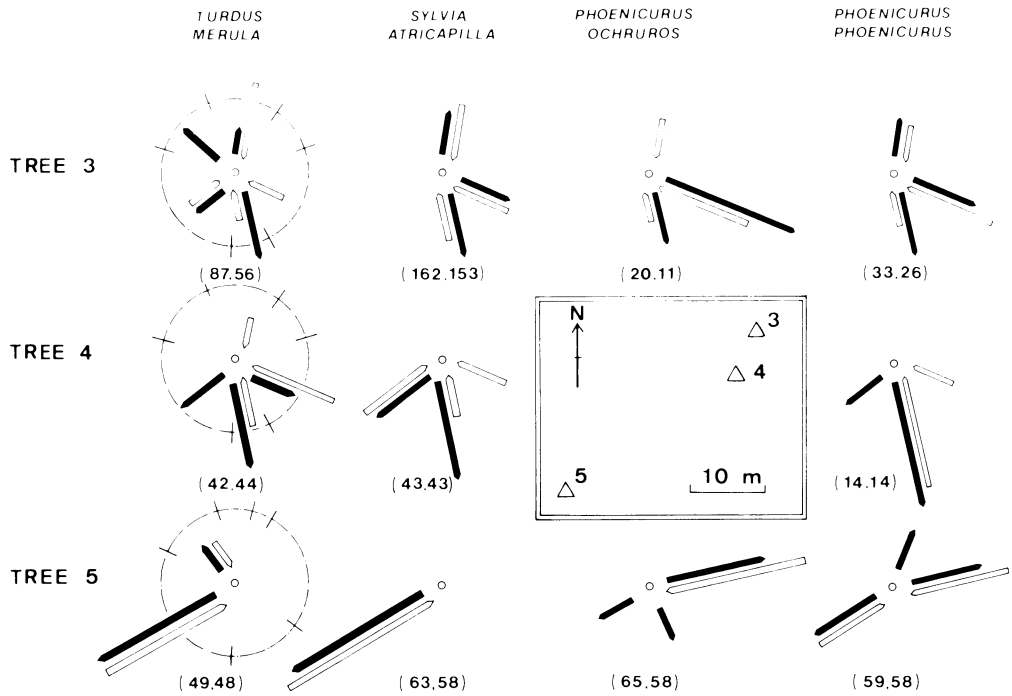

FIG. 4. Relative directionality of arrival (open bars) and departure (solid bars) flights at *P. mahaleb* study trees. Flight sectors from each tree are represented in the far left graphs. Only the most common flight directions, accounting for ≥75% of all observations, have been represented in each graph. The graph for *P. ochruros* in tree 4 has been omitted due to insufficient data, and inset shows the relative location of trees (triangles). Figures in parentheses represent number of observations on which the graph is based (first figure refers to arrival flights, second to departures).

relations between the relative use of every sector (departure flights) and the importance of each habitat component were obtained for every bird species. Correlation coefficients were simply used as measures of agreement, without further statistical inferences. The seven coefficients obtained for each species were then standardized ($\bar{x} = 0$; SD = 1), and the resulting figures used as indices of response to every habitat component (Fig. 5). The four species responded positively to a dense cover of shrubs <1 m high, and tended to avoid extensive open areas and dense pines. *T. merula* and *S. atricapilla* both favored sectors with greater cover of broad-leaved trees, and avoided pines at any density. The two *Phoenicurus* responded positively to sparse pines, with *P. ochruros* also favoring rocky substrates. As these results are based on information derived from departing flights, they reveal that different species tend to carry seeds to structurally distinct habitat patches.

Overall directional pattern of the seed flow originating from any tree appears thus to be determined by the action of two superimposed processes. First, interference from neighboring trees sets certain limits to the origin (and destination) of dispersers. And secondly, those birds eventually reaching the tree tend to select particular departure flight directions according to species-specific habitat preferences. Obviously, since the importance as seed vectors differs among species, the final pattern results from weighting each species' directional pattern by its relative contribution to the total amount of seeds transported. This is illustrated in Fig. 6, where it can be seen that overall directional patterns of seed dispersal at our study trees mostly reflect the particular flight patterns of the two major dispersers (*T. merula* and *S. atricapilla*) and the intertree interference effect.

DISCUSSION

Differential significance of dispersers to Prunus mahaleb

Bird species actually interacting with *P. mahaleb* (seed dispersers) are only a subset of the total species pool available in the habitat. The point our results serve to emphasize is that fruit-eating species in Roblehondo are not a random subset of available ones, and that bird size appears to be a major variable determining frugivory. Among species in taxa "predisposed" to fruit eating, only birds of certain sizes are able to utilize effectively the relatively large-seeded fruits of *P. mahaleb*. Among *P. mahaleb* dispersers there exists a size-related upper limit to the number of fruits ingested per feeding session, most likely set by gut size, as revealed by the significant regression

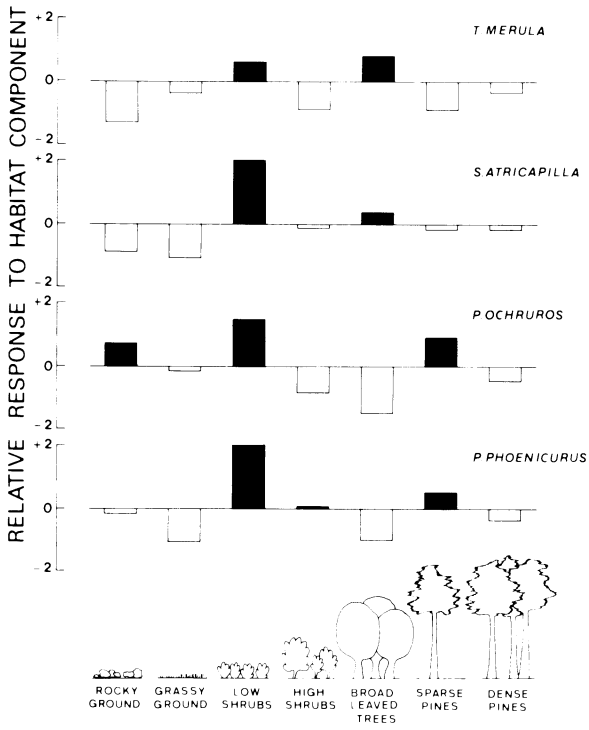

FIG. 5. Relative responses to each qualitative habitat component of the main *P. mahaleb* dispersers. See text for the meaning of the response index.

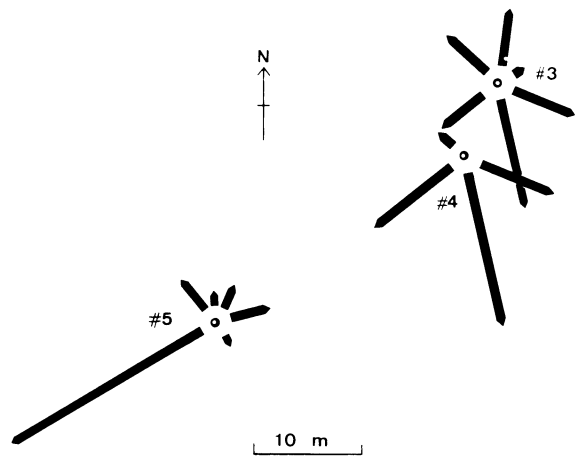

FIG. 6. Relative directional components of seed dispersal at study trees. Only those sectors accounting together for 75% of all dispersed seeds have been represented for each tree.

equations (Fig. 1). The upper limit for species <11 g is less than one fruit, so they are apparently unable to become frugivorous, although further limitations on fruit feeding derived from the relationship between gape width (probably correlated with bill width) and fruit diameter may be operating as well. Results thus suggest that whether or not a bird is a fruit eater in a specified context is to some extent determined by bird- and fruit-related size factors. In the case reported here, this produces a clear-cut discontinuity among the potential fruit consumers available in the area where the tree is growing.

Among species actually dispersing seeds, the overall significance of any of them to the tree is determined by the product of (1) a "quality" factor, the probability of seeds being dropped undamaged in a place where germination and growth to maturity are likely, and (2) a "quantity" factor, the number of seeds removed. The simple movement of seeds some distance away from the parent tree, thus decreasing local seed density, enhances survival (Janzen 1970, 1971*b*, 1972, Howe and Primack 1975, Salomonson 1978, Fowler 1979). Therefore, in this respect all four bird dispersers are beneficial to *P. mahaleb*, for they all fly away from the tree after feeding and void seeds in undamaged condition. The two *Phoenicurus*, however, dropped some fruits beneath the parent tree during their frequent unsuccessful feeding attempts and were also seen regurgitating seeds while perched in the trees. Due to behavioral interference, they spent much more time at the trees than strictly necessary to feed, thus increasing the probability of regurgitating seeds in situ. This behavior is detrimental to the plant, since almost all *Prunus mahaleb* seeds falling under the tree are destroyed by mice and deer. The behaviorally dominant and very efficient fruit harvesters *T. merula* and *S. atricapilla* appear to minimize the time spent at the trees and were never seen to drop any fruit, thus their behavior strongly favors successful seed dispersal.

Improved germination after passage through the digestive tract is a common feature in many bird-dispersed seeds (Krefting and Roe 1949); this may influence the quality of dispersal. This aspect has not been investigated in the present study but it can not be ruled out, since the beneficial effects of bird ingestion on seed germination have been demonstrated for *Prunus serotina*, a North American species closely related to *P. mahaleb* (Krefting and Roe 1949).

A third and probably most important factor affecting quality of dispersal is the occurrence of directional flight patterns after feeding as related to particular habitat preferences of the various disperser species. These patterns produce unhomogeneous seeding patterns (Howe and Primack 1975, Janzen et al. 1976, Lieberman et al. 1979). This effect must be particularly important in cases such as the present, in which plants grow in patchy habitats where survival of seeds probably differs among patches. The limited evidence available on the distribution of *P. mahaleb* saplings only allows us to state provisionally that, owing to grazing by ungulates, (1) a dense low-shrub cover appears to increase the probability of sapling growth up to shrub height without serious herbivore damage, and (2) large prereproductive saplings emerging above low-shrub level are subject to the heaviest browsing pres-

TABLE 7. Bird and plant perspectives of the *P. mahaleb* seed dispersal system, showing that bird species for which *P. mahaleb* fruits are important dietary elements are also most important to the plant. See text for further details.

	T. merula	*S. atricapilla*	*P. ochruros*	*P. phoenicurus*
Birds' view				
Energy-related efficiency	Very high	High	Low	Low
Time-related efficiency	Very high	Very high	Low	Very low
Importance of *P. mahaleb* fruits for food	High	High	Medium	Low
Plants' view				
Importance as disperser of *P. mahaleb*	Very high	High	Negligible	Negligible
Quality factor	Very high	Very high	Low	Low
Quantity factor				
Visitation rate	High	Very high	Low	Low
Seeds removed per visit	Very high	Medium	Low	Low

sure in the most open vegetation (lacking dense thickets of young *Q. ilex* trees). Similarly, it has been stated for *P. serotina* in North America that "practically all seedlings may be destroyed by rabbits or deer unless protected in some way" (Halls 1977). This considers only the decrease in seed survival due to ungulate damage, but invertebrate and rodent predation on seeds may be equally important in determining differential value of habitat patches (Janzen 1971*a*). Considering the flight patterns of dispersers, it may tentatively be suggested that (1) all bird species carry seeds to suitable habitat patches where early growth is likely, as all avoid open terrain and select actively areas covered by low shrubs, and (2) *T. merula* and *S. atricapilla* transport seeds preferentially towards areas where further growth up to a size most resistant to browsing is most likely, since both species select habitat patches covered by broad-leaved trees (mainly *Q. ilex*). Accordingly, *T. merula* and *S. atricapilla* are to be considered the "best" dispersers of *P. mahaleb* with regard to the quality factor mentioned above. They are also the best with regard to the quantity factor, for they disperse the bulk of seeds at every tree. The number of seeds dispersed by any species is simultaneously determined by the product of absolute abundance in the habitat, average frequency of visitation to the tree by individual birds, and number of seeds removed per visit. Independent data on the first two variables are not available in this study, but actual visitation rates observed at the trees result from their combined action.

Number of seeds removed per visit is correlated with body mass (Howe and Steven 1979, Jordano 1979, and present study), thus all else being equal, larger birds are better potential dispersers with regard to "quantity" of dispersal performed. But larger organisms are usually less abundant in any habitat (Hutchinson and Mac Arthur 1959, Van Valen 1973), resulting presumably in lower visitation rates. The product of visitation rate and the number of seeds removed per visit yields the absolute amount of seeds dispersed. Therefore, medium-sized birds with fairly high visitation rates are likely to disperse the most seeds. In the present study, *Garrulus glandarius* was by far the largest fruit eater, but it was so infrequent that its importance was totally negligible. *S. atricapilla* visited the trees more frequently than *T. merula* but, as the latter ingested many more seeds per visit, it is favored in the final balance. Similar results have been obtained in tropical studies by Howe and Steven (1979), Howe and Vande Kerckhove (1979) and Frost (*in press*), and in a Spanish mediterranean area by Jordano (1979). A complicating factor is the possible existence of numerical responses of birds to local fruit availability, producing an increase in the abundance of large-bodied species (Crome 1975). This may be a frequent mechanism enhancing the importance of larger dispersers, which is certainly the case with *T. merula* in the present study. Larger birds ranging over wider areas are most likely to detect local fruit availability and respond numerically.

Data relevant to the gradient of disperser importance to the plant are summarized in Table 7. Quantity- and quality-related values of the four disperser species go in the same direction and the ideal product of quality and quantity factors further amplifies interspecific differences. *T. merula* and *S. atricapilla* are by far the "key" dispersers, and the two *Phoenicurus* species have a negligible, and even partially detrimental effect on overall plant dispersal.

Differential significance of Prunus mahaleb *to the dispersers*

In southern Spain, *Phoenicurus phoenicurus* is mainly a spring and fall migrant which breeds very locally in mountain habitats (Herrera 1978*a*, Torres 1978). Breeding birds feed exclusively on insects, but fall migrants and postbreeding residents consistently ingest fruits in small quantities wherever available (Jordano 1979). Frugivory has been also reported elsewhere (Buxton 1950, Turcek 1961). *P. ochruros* is a fairly abundant resident on mountains, and a regular

wintering species throughout southern Spain. It appears to feed exclusively on insects throughout the year in all habitat types (Herrera 1978*b*), and the only exception known to us is the consumption of *Prunus mahaleb* drupes reported in this paper. *S. atricapilla* is abundant in most southern Spanish habitat types in autumn to winter, and a fairly abundant breeder in some areas above 1000 m. In autumn to winter its diet is based almost exclusively on fruits (Jordano and Herrera 1981), and in some habitats of the Sierra de Cazorla, mistletoe (*Viscum album*) berries are also ingested by breeding birds. Extensive frugivory of this species is well known both elsewhere in Europe (Turcek 1961) and in its African winter range (Moreau 1972), and central European populations have been shown to exhibit an endogenous rhythm in food preferences, with fruits preferred to insects in autumn to winter (Berthold 1976). In southern Spain fruits are consumed by *T. merula* in autumn to winter in most habitat types, with some populations feeding on fruits virtually year round (Jordano 1979, Herrera, *in press*). The strong tendency of this species to frugivory has been repeatedly documented elsewhere in Europe (e.g., Hartley 1954, Turcek 1961, Alonso and Purroy 1979). These data suggest that the overall tendencies to frugivory of the four species are essentially similar to those revealed at *P. mahaleb* trees, with *T. merula* and *S. atricapilla* relying heavily on *P. mahaleb* for subsistence and the two *Phoenicurus* species having fruits as a minor dietary element. The fact that most birds left the study site after fruit crop exhaustion also reveals that *Prunus mahaleb* fruits have a definite importance for the local persistence of dispersers.

The ability to depend to a large extent on *P. mahaleb* fruits must be related to the combined action of availability of alternate food and efficiency in harvesting fruits. Data on abundance of alternate food are not available, but the consideration of feeding efficiency alone supports the prediction that the most efficient fruit harvesters will show the highest dependence on fruits for food. "Efficiency" may be partitioned into energy-, time-, and risk-related components. Energy-related efficiency has to do with the energetic costs associated with ingesting a fruit-unit, which are related, among others, to the method used for feeding (costly hovering vs. inexpensive feeding from a perch), frequency of flights following aggressions, and foraging restlessness. The time-related component of efficiency relates to the percentage of successful feeding attempts, because as the number of fruits ingested per feeding session appears to be species specific, a higher frequency of unsuccessful attempts will increase total residence time at the tree, and decrease overall ingestion rate. Time-efficiency is likely related to predation risk. Abundance and diversity of bird predators in the study area suggest that there must be a heavy potential predation pressure on dispersers. Concentrations of birds at fruiting trees will probably attract the attention of predators (Howe 1977, 1979). Spending more time at the tree than necessary thus increases the probability of being preyed upon, and species minimizing the time necessary to ingest a fruit load are also minimizing exposure to predators (Howe 1979). Relevant data on the gradient of fruit dependence among dispersers are summarized in Table 7. *T. merula* shows by far the greatest efficiency in fruit feeding and it depends heavily on *P. mahaleb* fruits for food. In the opposite extreme, the very inefficient *Phoenicurus* depends much less strongly on fruits. Degree of dependence on fruit for food must be closely correlated with bird reliability to the plant as a disperser (Howe and Estabrook 1977); thus *S. atricapilla* and *T. merula* are probably the most reliable dispersers, and *Phoenicurus* the least, to *Prunus mahaleb*. Differential reliability revealed in our study is further supported by the fact that the former two species have been mentioned among those eating *P. mahaleb* fruits in central Europe, whereas neither *Phoenicurus* species has been recorded (Turcek 1961).

Bird- and plant-related coevolutionary gradients

Plant-disperser coevolution is the result of reciprocal exploitation by the two parties involved. Plants have their seeds dispersed and dispersers get a nutritive reward. There are associated costs to both plant and disperser. The former invests energy and nutrients in excess of those necessary to produce seeds alone. The disperser has to ingest a certain amount of useless material which increases body mass, and hence energy expenditure in locomotion. Plant and disperser are thus subject to counteracting selective pressures and continuous feedback between them will lead to compromise situations in nature (Snow 1971). The variety of compromises which have evolved has been suggested by some authors to fall somewhere between the two following extremes: a high-quality, costly fruit to "pay" for the services of a reliable disperser ("specialist"), as opposed to a poor fruit which rewards the dispersal performed by unreliable dispersers ("opportunist") (Snow 1971, McKey 1975, Howe and Estabrook 1977). Two extreme plant types have been associated with these bird extremes: Model 1 plants produce relatively large seeds with a high nutrient reward, with extended fruiting periods, and Model 2 plants produce many small-seeded fruits of low nutritive reward over short fruiting seasons (Howe and Estabrook 1977). Current theory predicts that the interaction between the disperser- and plant-related factors generates a new gradient as follows: Model 1 plants are mainly dispersed by specialists on one extreme, and Model 2 plants are dispersed by opportunists on the other extreme of the gradient (Howe and Estabrook 1977). Two points are crucial to the model. First is the degree of fruit dependence of disperser species, which determines their reliability. Second are

the different degrees of dependence of a plant species on various dispersers differing in dispersal efficiency. If a plant species depends most heavily on disperser species for which, in turn, the fruits of that plant are very important for subsistence, then it is usually considered that the system is highly coevolved and it is close to the Model 1-specialist extreme. If a plant species depends mainly on dispersers for which the fruits are relatively unimportant, theory predicts the system is most likely characterized by Model 2 plant and opportunist dispersers. These predictions emanate from Howe and Estabrook's (1977) model for tropical habitats. The consideration of these gradients usually forms the core of models relative to plant-frugivore coevolved systems (Snow 1971, McKey 1975, Howe and Estabrook 1977, Howe and Vande Kerckhove 1979, Howe and Steven 1979).

In terms of the plant-related gradient, *Prunus mahaleb* has all the attributes of a typical Model 2 plant, for it shows high fecundity and a short fruiting period. Furthermore, the flesh of the fruit has an extremely low nutritive value. Compare dry-mass figures for *P. mahaleb* pulp (3.2% fat and 2.8% protein) with, for instance, mean values of 10.2% fat and 4.9% protein for pulps from 21 other southern Spanish bird-dispersed species (C. M. Herrera, *personal observation*), and 19.8% fat and 8.1% protein for 12 species in a South African subtropical dune forest (Frost, *in press*). Theory would predict that *P. mahaleb* is dispersed by opportunist species relying little on fruit for food and performing low-quality dispersal. Our results do not confirm these predictions. With regard to the specialist-opportunist continuum, it seems reasonable to consider the two *Phoenicurus* species as approaching the opportunist end, while *T. merula* and *S. atricapilla* are relatively close to a hypothetical specialist extreme. Therefore, *Prunus mahaleb* possesses an efficient dispersal system based on the production of many low-quality fruits. A similar finding has been provided by the study of the dispersal system of *Rubus ulmifolius* (Rosaceae), an early successional species, in which the bulk of dispersal is accomplished by a few reliable specialists (*T. merula* and *S. atricapilla* among them) (Jordano 1979). The fairly large seed of *P. mahaleb,* the fourth largest in size among 49 common southern Spanish species of bird-dispersed plants (C. M. Herrera, *personal observation*), should have, according to theory, an associated nutrient-rich flesh. This is not the case, providing a further conflicting point.

Further temperate studies are not available for comparison, but the findings in the present study suggest that the nature of the correlation between plant- and bird-related gradients in temperate systems may differ substantially from that suggested by tropical-based studies. The gradients themselves undoubtedly do exist in temperate areas. The bird-related gradient has been illustrated in the present study (see also e.g., Salomonson 1978), and the plant-related one may be exemplified in southern Spain by *Pistacia lentiscus* (Anacardiaceae), *Viburnum tinus* (Caprifoliaceae), and *Olea europaea* (Oleaceae) at the Model 1 extreme (long fruiting season, protein- and/or oil-rich fruits, thin pericarp, large seed), and *Prunus mahaleb* and *Arbutus unedo* (Ericaceae) at the Model 2 extreme (very short fruiting season, carbohydrate-rich fruits, thick pericarp) (C. M. Herrera, *personal observation*). Probable differences between tropical and temperate habitats are the range of gradients and the nature of their correlation, and consequently the type of relationship between bird and plant types. The number of species available to a European or North American tree as potential dispersal agents is certainly less than the number available to a tropical plant, and the morphological and physiological diversities available are also likely to be far more restricted in temperate than tropical habitats. The suggested correlation of bird- and plant-related gradients in the tropics results from considering intraspecific competition for avian dispersers through analysis of the influence of crop size differences on dispersal success (Howe and Estabrook 1977). Discrepancies in the nature and/or strength of the suggested relationships found in the present study may reflect lower levels of intraspecific competition for dispersers (but see Herrera 1981), more severe environmental constraints limiting the evolution of rich-pericarp fruits, lower diversity of available dispersers, greater likelihood of specialization among a few species of birds, and differences in the absolute and relative abundances of reliable and opportunist dispersers. These comparative aspects have been not explored in quantitative ways and further work on temperate systems is urgently needed to document to what extent tropical vs. temperate differences suggested in this paper are widespread. Further tropical studies simultaneously considering the plant vs. bird aspects of the interaction are also essential to test effectively whether the suggested correlation between plant- and bird-related gradients actually conforms to model predictions.

Acknowledgments

Thanks are due to J. A. Carrera and J. Cavanillas, of the Spanish Instituto para la Conservación de la Naturaleza, for permission to work in Cazorla and provision of housing facilities in Roblehondo. Dr. P. G. H. Frost kindly allowed access to unpublished material, J. Herrera assisted efficiently with fruit skin microphotographs, and H. Pringle checked the English. A. Martín assisted with ash determination, and the remaining analyses of fruit pulp were carried out by Dra. A. García at the Sección de Praticultura, Centro de Edafología y Biología Aplicada, CSIC, Salamanca. Dr. D. W. Snow and two anonymous reviewers made helpful comments on the manuscript. Above all, we are indebted to Myriam for invaluable assistance with field work, solid patience with authors' behavior, and careful nursing and cooking. Had it been not for her help, our field work would not have been successfully accomplished in such a harsh July environment. This research was supported financially by the Estación Biol-

ógica de Doñana, Consejo Superior de Investigaciones Científicas.

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