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Marcelino Fuentes

Diets of fruit-eating birds: what are the causes of interspecific differences?

Abstract Differences in fruit choice among the bird species of a Spanish shrubland were related to the size of fruits and to the lipid content of pulp. Lipid-rich fruits were selected by the bird species with slower food passage rates through the digestive tract. These bird species also fed frequently on insects and seeds. Bird species with faster food passage rates fed less on insects and seeds, and ate mainly fruits with pulp poor in lipids (rich in sugars and water). Studies of digestion in birds indicate that lipids require slower food passage rates for efficient digestion and intestinal transport than simple sugars. The available evidence indicates that the European bird species that show stronger preferences for lipid-rich fruits are no better as seed dispersers, from the point of view of the plants, than species choosing lipid-poor fruits. Thus, the degree of frugivory of birds, their fruit choice patterns and their effects on seed dispersal do not seem to be related to each other in the ways expected by the early models of the evolution of fleshy fruits.

Key words Bird · Digestive physiology · Fleshy fruit Frugivory · Lipid

Introduction

It has been suggested that interspecific variation in traits (such as color or pulp constituents) of fleshy fruits eaten by birds has originated, at least in part, in response to selective pressures exerted by different sets of avian consumers (Snow 1971; McKey 1975; Howe and Estabrook 1977). For this to be true it is necessary, but not sufficient, that bird species differ consistently in their

M. Fuentes[1]
Area de Ecoloxía, Facultade de Bioloxía, Universidade de Santiago, E–15706 Santiago de Compostela, Spain

Present address:
[1] Department of Range Science and the Ecology Center, Utah State University, Logan, UT 84322-5230, USA

preferences for different kinds of fruits. Differences in fruit choice patterns among bird species have been attributed to fruit and seed size (Pratt and Stiles 1985; Wheelwright 1985; Jordano 1987a; Levey 1987a; Dowsett-Lemaire 1988; Debussche and Isenmann 1989), fruit color (Willson et al. 1990), chemical composition of the pulp (Crome 1975; Herrera 1984a; Johnson et al. 1985; Levey 1987b; Borowicz 1988; Jordano 1988; Lambert 1989), the presence of protective structures (Pratt and Stiles 1985; Davidar 1987; Restrepo 1987) and the position of fruits on the plants (Moermond and Denslow 1983; Levey et al. 1984; Santana et al. 1986; Cuadrado 1988; Loiselle and Blake 1990). The bird traits involved in these choice patterns include gape size (e.g. Wheelwright 1985), perceptual mechanisms (Willson and Whelan 1990), digestive physiology (e.g. Levey 1987b; Levey and Grajal 1991; Bosque and Parra 1992; Place and Stiles 1992), foraging behavior (e.g. Pratt and Stiles 1985) and locomotor anatomy (e.g. Moermond and Denslow 1983; Loiselle and Blake 1990). The few community-wide studies undertaken so far have established the importance of fruit size (gape size) and fruit accessibility (locomotor structures) in fruit choice, but still a large fraction of the interspecific variation in fruit choice remains unexplained (e.g. Hartley 1954; Snow and Snow 1971; Sherburne 1972; Crome 1975; Sorensen 1981; Herrera 1984a; Wheelwright et al. 1984; Innis 1989; Loiselle and Blake 1990; Boddy 1991).

In this study I try to assess the role of several traits of birds and fruits in the differences in fruit diet among the birds of a northwestern Spanish shrubland. The chosen site holds plant species with fruits differing greatly in several traits, most notably in lipid content of pulp. It has been hypothesized that the fast rate of food processing by most frugivores is suitable for assimilating simple sugars but may pose problems in dealing with lipids (Levey and Grajal 1991; Bosque and Parra 1992), and thus it may limit the inclusion of lipid-rich fruits in the diet. A specific purpose of this study is to look for correlates of consumption of lipid-rich versus lipid-poor fruits among bird species.

In early models for the evolution of bird-dispersed plants it was proposed that fruits with lipid-rich pulp (and presumed associated characteristics such as large size and the possession of a single seed) had evolved to maximize the quality of seed dispersal, by attracting a few, highly frugivorous, specialist bird species (Snow 1971; McKey 1975; Howe and Estabrook 1977; see also Howe 1993). According to these models, "low-quality" fruits (small, with many small seeds, and watery, succulent pulp) would be associated with "low-quality" dispersal performed by a large set of opportunistic frugivores. Another purpose of this study is to examine how the degree of frugivory of birds, their fruit choice patterns and their effects on seed dispersal are related to each other.

Methods

Study site

This study was done in a thorny shrubland in Mumao, near La Barosa (province of León, 42° 30'N, 6° 51'W, at 550 m a.s.l.), an area of Mediterranean climate. The shrubland I chose to study occupied a 3-ha oldfield surrounded by a dense shrubland composed of *Quercus rotundifolia* and *Arbutus unedo*.

I estimated the percentage cover of woody plants by annotating the presence or absence of each species in 329 points randomly placed throughout the site. More than 85% of the ground is covered with woody plants, mostly 2–3 m tall. The most abundant are *Quercus rotundifolia* and several fruit-bearing shrubs (Table 1). I found 16 fruit-producing species, mostly deciduous shrubs but also one woody vine (*Lonicera periclymenum*) and two herbs (*Fragaria vesca* and *Tamus communis*).

Several taxa in the genus *Rosa* appeared in the plot, *R. micrantha* being by far the most abundant. These taxa were almost indistinguishable with respect to vegetative and reproductive characteristics, including fruiting phenology (Fuentes 1992). As their taxonomic status is still dubious I treat them as a single taxon.

Fruit phenology and abundance

To estimate the seasonal availability of fruits I periodically (usually every 6–10 days) counted fruits on tagged branches of at least eight individuals of each species from June 1989 until no fruits remained on the plants (April 1990). In some species, this many plants were available for study: only two clones of *Cornus sanguinea* and one individual each of *Prunus mahaleb* and *Pistacia terebinthus* fruited in the plot. For the six most abundant species (Table 1) the number of fruits followed ranged from 754 to 2159. For the rest of species, all or nearly all fruits produced in the plot were followed. To estimate the absolute number of fruits produced in the plot I once counted all fruits (ripe and unripe) of each species in 215 sites, each approximately 3.5 m² in area, distributed throughout the plot. For some species I directly counted all fruits or infructescences present in the plot. To get an estimate of the seasonal variation in fruit abundance I combined the figures thus obtained with the data gathered in the periodic counts (see e.g. Herrera 1984a). A detailed account of the results obtained can be found in Fuentes (1991).

Bird abundance and diet

I studied the seasonal variation in bird abundance by mist-netting (see e.g. Herrera 1984a; Levey 1988; Loiselle and Blake 1991). I opened four 12-m nets during 1–3 consecutive days every 5–12 days from July to October, every 15 days in November and once (2 days) at the end of December 1989. Nets were kept open from about half an hour after dawn until dusk (i.e. for 8–12 h). I also made direct counts of birds while I walked along a 340-m trail that crossed the plot. I made four or five censuses every half month between July and November and five during December 1989, always within 2 h after dawn. Mist-net captures and direct counts yielded similar results (Fuentes 1992).

I studied the diet of birds by analyzing the fecal droppings obtained from mist-netted birds (see e.g. Herrera 1984a). The droppings were dried and later analyzed with a dissecting microscope. In each dropping I visually estimated the percentage volume occupied by each fruit species, by other vegetable matter and by animal remains, with a 10% accuracy. I identified fruit species by the seeds and by examining the epicarp remains with a microscope. I compared the latter with a collection of microphotographs in which cell size and shape, stomata and hairs could be recognized. I was unable to identify seed remains in droppings from granivorous birds.

From each netted bird I took measures of body mass and length of wing, tail, tarsus, and bill from feathers to tip, and bill depth and width at the anterior part of the narines.

Statistical analyses

I conducted a principal component analysis (PCA) on aspects of the morphology and digestive physiology of the birds in order to find relationships among these variables and patterns of frugivory. I included the morphological variables just mentioned above, as well as gape width and food passage rate through the digestive tract (FPR), which were taken from Herrera (1984b) and Jordano (1984, 1987a). I divided all variables, except intestine length and FPR, by the cube root of body mass in order to eliminate the effect of size, and log-transformed them. The intestine length was divided by the square root of body mass and log-transformed (see Herrera 1986). Degree of frugivory (DF) is here defined as the percentage in volume of fruit remains in the droppings obtained from mid-August until the end of October. During this period all fruit-eating bird species were present in the plot and showed quite constant patterns of frugivory (Fuentes 1992). I arcsine-transformed DF for the analyses.

To look for patterns of variation in bird diets, I conducted a PCA on the proportions (arcsine-transformed), relative to total volume of fruit remains, made up by each of the 12 main plant species in the droppings of the nine main fruit-eating bird species studied.

Additionally, I ran a randomization test to look for the most significant differences in fruit diet composition among these species. The analysis was designed to eliminate differences in diet arising from differences in the phenology of bird species in the plot. I distributed the droppings into 18 temporal groups, each comprising the droppings collected in each mist-netting period of 1–3 consecutive days. The randomization procedure consisted of reassigning the droppings of each temporal group randomly and without replacement to the bird species. The number of droppings of each period assigned to each bird species was equal to that actually collected for that species in that period. For example, suppose a total of ten droppings, six of them from bird species A and four from species B, were obtained in a given period. The randomization procedure would randomly assign six droppings to species A and the rest to species B. A randomization run consisted of doing this for all 18 periods. Then, I computed the proportions (volume relative to total volume of fruits) made up by each of the 12 main fruit species in the randomized set of droppings of each bird species. I generated 10 000 randomized data sets, and counted the number of times the random proportions were smaller than, greater than or equal to the proportions actually observed.

I conducted separate PCAs on several morphological and nutritional characteristics of the fruits that might have influenced

their consumption by birds. This was done for the 12 main plant species. In the first PCA, I included maximum diameter of fruit, fruit fresh mass, dry mass of pulp, dry mass of seeds, number of seeds, dry mass of each seed, ratio of dry mass of pulp to dry mass of seeds (pulp to seed ratio thereafter), dry mass of pulp per seed (all these variables log-transformed) and relative yield (dry mass of pulp relative to fresh mass of the whole fruit; arcsine-transformed). In the second, I included the percentage of water in the whole fruit [as an indirect estimate of the proportion of water in the pulp; see Herrera (1987) for a thorough justification of this], and the proportion of dry mass of pulp made up by lipids, proteins, fiber and non-structural carbohydrates (these four variables arcsine-transformed). All data were taken from Herrera (1987). I used data from *Rosa canina* for *Rosa micrantha*. These two fruits are very similar morphologically (M. Fuentes, unpubl data). No data were available for the pulp composition of *Rubus ulmifolius*.

In each PCA I selected those components with eigenvalues greater than 1.
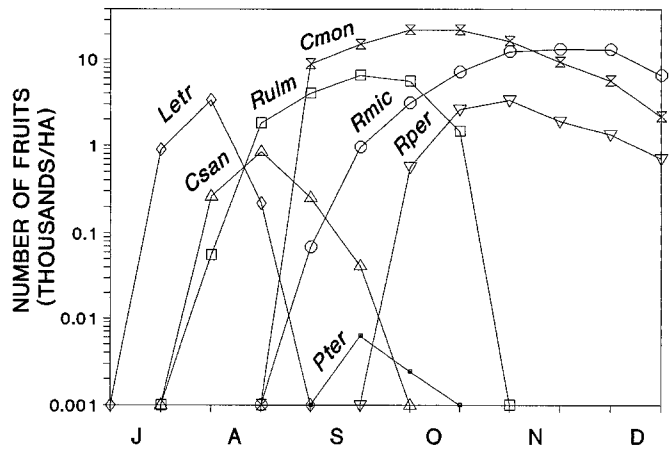

Fig. 1 Availability of fruits of the main plant species in the study plot. Plant species are denoted with the first letter of the genus and the first three letters of the species epithet (see Table 1)

Results

Fruit and bird abundance

The fruiting phenology of the main fruit-bearing plant species in the study plot is shown in Fig. 1. A few fruits of *Prunus mahaleb* were available at the end of June and the beginning of July and a few fruits of *Daphne gnidium* were available from September onwards. Most fruits left on the plants after December were not eaten by birds, by then very scarce in the plot (see below), and ultimately dried up. The maximum number of species in fruit occurred in late September and early October. As a whole, approximately 86 000 fruits/ha ripened during the 1989–1990 fruiting season, with five species accounting for most of this (Table 1). This production was highly concentrated in the 3-ha plot: fruits were very scarce in the evergreen oak shrubland surrounding it (Fuentes 1991). The maximum number of fruits occurred in late October.

During the 5 months I opened mist nets I captured 829 birds of 28 species (Appendix). The maximum number of captures was in the first half of August, with an

average of 36 captures/day, and the minimum was in late December with an average of 3.5 captures. The maximum number of species captured occurred in September, with 22 species, and the minimum in December, with 4. More than half of species and of individuals at any time were of fruit-eating birds (see below).

Degree of frugivory

I analyzed 627 droppings from 25 species of birds. Fruit pulp, seeds and invertebrates were the main food sources in the plot during the period July–December 1989 (Table 2). Fifteen species fed on fruit pulp. All of them also ate invertebrates and two also ate seeds. *Pyrrhula pyrrhula* and *Fringilla coelebs* fed on the seeds of fleshy fruits (at least of *Lonicera* and *Rubus*), but I could not identify the remains appearing in their droppings. The droppings of another seven species contained only arthropod remains, and the only two droppings

Table 1 Percent cover, annual fruit production (ripe fruits/ha) of the plant species producing fleshy fruits in the plot and some characteristics of fruits discussed in the text. (*Rosa* spp. are mainly *R. micrantha*. + Plants or fruits present in very small numbers in the plot; P/S pulp to seed ratio)

	Cover	No./ha	Diameter	P/S	Lipid
Crataegus monogyna	46.2	31000	9.3	1.4	2.3
Rosa spp.	14.9	23000	9.2	1.8	2.8
Rubus ulmifolius	12.5	13000	14.6	2.4	—
Lonicera etrusca	12.2	12000	6.5	1.5	2.3
Rubia peregrina	12.5	5000	6.1	1.1	9.9
Cornus sanguinea	1.8	1000	6.8	0.7	24.9
Pistacia terebinthus	0.3	150	5.8	0.8	55.6
Daphne gnidium	1.8	100	5.0	1.1	2.6
Tamus communis	+	50			
Prunus mahaleb	0.6	10	8.3	0.6	3.2
Lonicera periclymenum	+	+			
Prunus spinosa	1.2	+			
Fragaria vesca	+	+			
Arbutus unedo	14.6	—	17.1	20.9	2.9
Phillyrea angustifolia	+	+	—		
Viburnum lantana	+	—	6.4	0.8	2.6
Malus sylvestris	—	—	30.3	31.7	5.4

Table 2 Average percent volume per dropping of animal (mainly insects), fleshy fruit and other plant (mainly seed contents) remains in the birds studied, and some other characteristics of birds that are discussed in the text. Only bird species with more than three droppings are included. (DF degree of frugivory, as defined in the text; n number of droppings analyzed; + Frequency lower than 0.5%. Species abbreviations consist of the first letter of the genus and three first letters of the species epithet: see Appendix)

|		% in diet				Body mass (g)	Gape width (mm)	Food passage rate (mm/min)
	n	Animal	Fruit	Plant	DF			
Satr	124	19	79	2	89	16.9	8.5	4.3
Tphi	7	9	91	0	89	65.4	13.7	8.3
Sbor	21	16	84	0	84	19.8	8.6	3.5
Tmer	32	25	75	0	75	86.9	13.4	3.3
Erub	170	52	43	5	48	16.5	8.0	5.0
Pcae	47	49	36	15	46	10.5	5.2	1.7
Scan	25	85	13	2	46	9.7	6.3	4.1
Fhyp	17	76	24	0	24	13.2	7.9	2.3
Pmaj	7	67	9	24	20	17.3	7.3	2.1
Lmeg	9	86	14	0	14	21.6	9.2	–
Pcol	29	95	2	3	4	7.5	5.6	1.3
Pmod	22	50	+	50	+	17.6	6.8	2.0
Rign	31	100	0	0	0	5.0	5.1	2.4
Ptro	13	100	0	0	0	9.5	5.5	1.5
Ttro	7	100	0	+	0	9.5	6.2	3.3
Acau	20	99	0	1	0	7.2	5.3	–
Fcoe	6	7	–	93	0	21.0	8.0	2.4
Ppyr	27	1	–	99	0	20.4	10.2	–
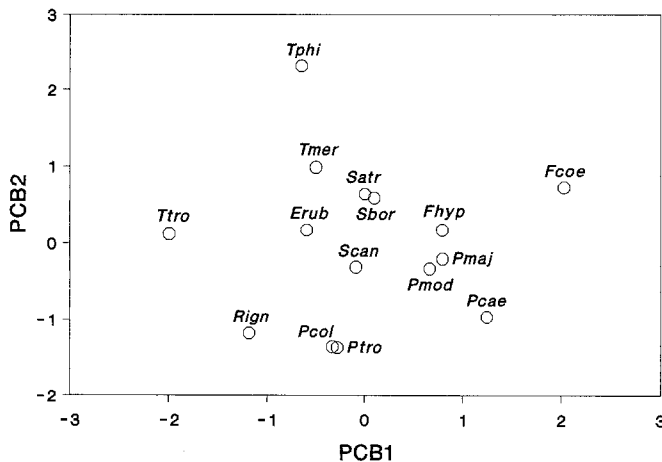
Fig. 2 Position of the bird species in the plane defined by factors correlated with bill shape and locomotor structures (*PCB1*), and body size, gape width, food passage rate through the digestive tract and degree of frugivory (*PCB2*) (see Table 3). Bird species are denoted with the first letter of the genus and the first three letters of the species epithet (see Appendix)

Table 3 Results of a principal components analysis conducted on several bird traits. Pearson correlations (>0.25, n = 15) between principal components and the variables included in the analysis (relative importance in the diet of each bird species) and with DF, and percent variances associated with each component are shown

	PCB1	PCB2	PCB3
Variance	35%	22%	15%
Wing length	0.5		0.7
Tail length	0.6		0.5
Tarsus length	−0.7	−0.5	0.3
Bill length	−0.8		
Bill width	0.9		
Bill depth	0.8		−0.3
Gape width	−0.3	0.7	0.5
Intestine length	0.5		−0.3
Food passage rate	−0.3	0.8	
Body mass		0.8	
DF	−0.02	0.63	0.39

available from *Carduelis chloris* contained only seed remains.

There was a slight significant correlation between the temporal variation of the importance of fruits (percent volume) in the diet of the birds and fruit abundance (Spearman rank correlation $r_s = 0.6$, $P < 0.05$, $n = 11$ half-months). However, fruit consumption in absolute terms (taking into account both the importance of fruits in the diet of the birds and the biomass of the latter in the habitat) was not correlated with the abundance of fruits ($r_s = 0.4$, $P > 0.1$), due to the decline in bird abundance in autumn.

Three principal components account for 72% of the variance in the bird traits analyzed by PCA (Table 3, Fig. 2). The birds with relatively long wings and tails,

short tarsi, and short, wide, and deep bills show high values on the first principal component (PCB1). The second component is positively correlated with body mass, gape width and FPR values. Of these three factors, only PCB2 is significantly correlated with DF (Pearson correlation $r = 0.63$, $P = 0.012$, Bonferroni-corrected $P = 0.035$, $n = 15$). Thus, the birds of larger size, faster food passage rate and wider gape tended to be the most frugivorous (as defined here). The birds that fed on the pulp without swallowing fruits whole (*Parus caeruleus*, *Parus major* and *Phylloscopus collybita*) had low values of both PCB2 and DF relative to the other frugivorous species.

Taking the nine main species of fruit-eating birds (>6 droppings analyzed, Table 4) there was a slight significant correlation between the degree of frugivory and the number of fruit species detected in their droppings ($r_s = 0.7$, $P < 0.05$, $n = 9$). There were no significant corre-

Table 4 Relative contribution, in percent volume (rounded to the integer), of each fruit species to the diet of each bird species. Marked proportions are significantly (P<0.001) greater (+) or smaller (−) than expected (randomization tests, see text). n number of droppings in which each fruit species appeared. Species abbreviations consist of the first letter of the genus and three first letters of the species epithet: see Appendix and Table 1)

	n	Fhyp	Pcae	Tmer	Erub	Scan	Sbor	Satr	Tphi	Lmeg
Pter	76	6	+18	0	1	0	9	4		
Cmon	45		0	+36	−1			4	20	
Csan	76	+17	−	1	4		2	4	3	3
Rulm	227	−1	18	27	23	9	67	34	27	10
Vlan	33			0	+5			2		
Letr	52			0	−1	4	2	20		0
Rper	45			5	2		3	8	14	
Msyl	52	0			+4	0	1	1	14	
Aune	24			0	2			0	13	
Rosa	7			6			0	1		
Dgni	7							1		
Pmah	2							0		

Table 5 Results of a principal components analysis conducted on the relative importance of each fruit species (main 12 species) in the diet of each bird species. Pearson correlations (>0.25, n=12) between principal components and the variables included in the analysis, and percent variances associated with each component are shown

	PCC1	PCC2
Variance	59%	16%
Erub	0.9	
Fhyp		0.7
Lmeg	0.9	
Pcae	0.7	0.3
Satr	0.9	
Sbor	1.0	
Scan	0.9	
Tmer	0.6	−0.6
Tphi	0.6	−0.6

lations between this latter variable and any of the principal components of Table 3, the number of droppings analyzed for each species or the number of half-months from which droppings were obtained.

Fruit choice

Most fruit-eating bird species in the habitat fed mainly on *Rubus* fruits, completing their frugivorous diet with smaller quantities of other fruits (Table 4). *Cornus* and *Rubus* were eaten by the greatest number of bird species. All subsequent analyses concern the species with greater sample sizes, which are shown in Table 4.

Two factors were extracted from the PCA of the relative frequencies of each plant species in the diets of the different birds (Table 5). Together these factors explained 75% of the variance. The plant species that appeared most frequently in the droppings of birds, notably *Rubus*, have higher values in the first component (PCC1; Fig. 3a). The second component correlates with the relative importance of each fruit in the diets of *Ficedula hypoleuca* (positively) and of *Turdus merula* and *T. philomelos* (negatively). *Cornus* and *Pistacia*, whose fruit remains were relatively more important in the droppings of *F. hypoleuca*, have the highest scores on
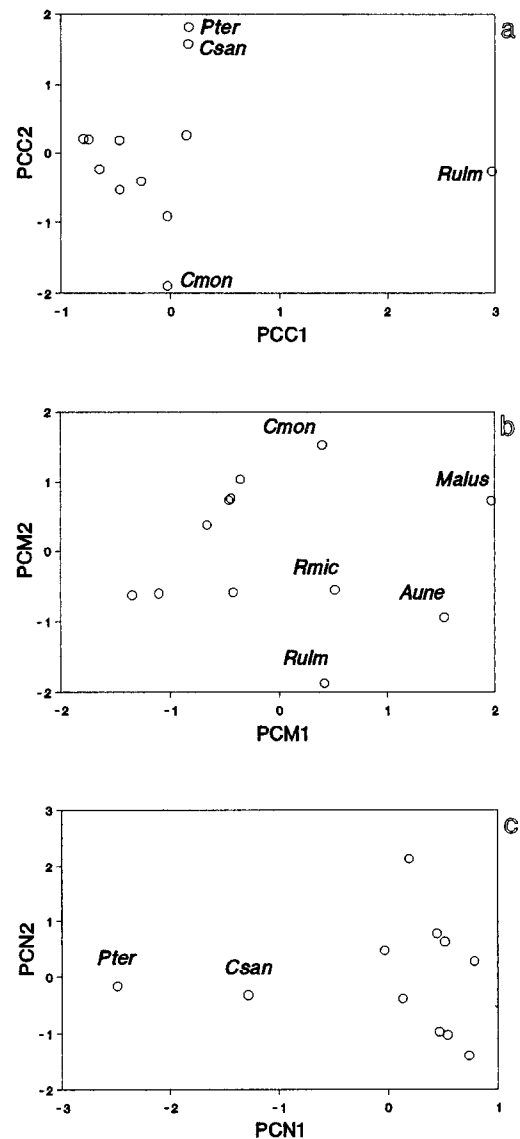

Fig. 3 Position of the plant species in the planes defined by: **a** factors related to fruit consumption intensity (*PCC1*) and fruit choice (*PCC2*) by birds (Table 5); **b** morphological characteristics of the fruits (Table 6); and **c** nutritional factors associated with the lipid versus sugar (*PCN1*) and fiber (*PCN2*) content of the pulp of fruits (Table 7). Plant species are denoted with the first letter of the genus and the first three letters of the species epithet (see Table 1)

Table 6 Results of a principal components conducted on several morphological traits of fruits of the 12 main species eaten by birds. Pearson correlations (>0.25, $n=12$) between principal components and the variables included in the analysis, and percent variances associated with each component are shown

	PCM1	PCM2
Variance	60%	25%
Diameter	0.9	
Mass of fruit	1.0	
Dry mass of pulp	1.0	
Dry mass of seeds	0.7	0.4
Number of seeds	0.6	-0.7
Dry mass of each seed		1.0
Pulp to seed ratio	0.9	
Dry mass of pulp per seed	0.7	0.7
Relative yield	0.7	

Table 7 Results of a principal components conducted on several nutritional fruit traits of the species present in the plot. Pearson correlations (>0.25, $n=11$) between principal components and the variables included in the analysis and percent variances associated with each component are shown

	PCN1	PCN2
Variance	55%	28%
Lipid	-1.0	
Protein	-0.7	0.5
Non-structural carbohydrates	0.9	0.4
Fiber	0.4	-0.8
Water	0.5	0.6

this factor, and *Crataegus*, which was frequent in *Turdus* droppings, has the lowest.

The randomization test detected 20 (20%) significant departures from randomness at the 0.05 level (two-tailed), among the 96 fruit × bird interactions compared (12 of the 9 × 12 = 108 interactions were forbidden because of unmatched phenologies of bird and fruit species). The significant cases involved *E. rubecula* (6 fruit species, out of 12 possible comparisons, were eaten significantly more or less than expected), *Parus caeruleus* (5 of 11), *T. merula* (3 of 12), *F. hypoleuca* (2 of 10), *Sylvia cantillans* (2 of 10) and *S. atricapilla* (2 of 12). Of these, 16 were also significant at the 0.01 level and 9 of these also at the 0.001 level. Only the most significant departures from randomness will be considered further (Table 4), in order to avoid Type I errors associated with the high number of comparisons made.

The PCA on the morphological characteristics of fruits extracted two factors that explained 85% of the variance in the traits analyzed (Table 6, Fig. 3b). The first is associated with several measures of the size of fruits and the second is correlated positively with both the mass of seeds and the quantity of pulp per seed, and inversely with the number of seeds. The pulp-to-seed ratio increases with size among the plant species studied here.

The PCA on the nutritional characteristics of fruits extracted two factors that explained 83% of the vari-

ance (Table 7). The first factor, correlated with the quantity of lipids and proteins versus non-structural carbohydrates, neatly sets *Cornus* and *Pistacia* (which have the two most lipid-rich fruits, see Table 1) apart from the rest of species (Fig. 3c). This factor is significantly correlated with PCC2 ($r=-0.74$, $P=0.009$, two-tailed, $n=11$).

I tested for correlations between the importance of each fruit species (the nine species that appeared both in fruit counts in the study plot and in droppings) in the diet of birds and their availability in the plot. The availability of fruits was determined for each bird species taking into account the seasonal distribution of their droppings. The index used was the sum of the products of the number of droppings from each netting period by the abundance of each fruit species in the corresponding dates. There was a significant rank correlation only in the case of *T. merula* ($r_s=0.94$, $P<0.0005$, Bonferroni-corrected $P<0.005$, $n=9$).

Discussion

Only the fruits of a few species, particularly those of *Rubus*, were quantitatively important in the diets of birds. However, there were some pronounced differences in fruit diet among bird species. I will discuss the most significant ones (Table 4, Fig. 3a). *F. hypoleuca, P. caeruleus* and *T. merula* showed strong relative preferences for the fruits of *Cornus, Pistacia* and *Crataegus. F. hypoleuca* and *P. caeruleus* significantly avoided those of *Rubus* and *Cornus*, respectively. *Erithacus rubecula* also showed statistically significant preferences for *Viburnum* and *Malus* fruits, which are not readily interpretable with the available data. *E. rubecula* avoided the fruits of *Lonicera*, which ripened at a time when this bird species was feeding mainly on insects, and *Crataegus*. The remaining interspecific differences in fruit diet were much less important (Fig. 3a). Some of them were associated with differences in the phenology of the bird species in the plot. Thus, the fruits of *Lonicera* were relatively important in the diets of *S. atricapilla* and *S. cantillans* because of the high relative abundance of these birds during the fruiting season of *Lonicera* (see Fig. 1 and Appendix; direct counts revealed patterns of abundances of *Sylvia* very similar to those of mist-net captures). The same happened with *T. philomelos* and autumn-fruiting plants.

Fruit production varies greatly among years and sites in the area of the present study, and the relative proportions of fruits of different species vary accordingly (Fuentes 1991, and pers. obs.). Bird populations also vary spatially and temporally, with important consequences for fruit-bird interactions (Fuentes 1990; Guitián et al. 1992). For this reasons, the results of this study may also vary in important ways. However, at least some of the most significant patterns just described seem to be quite general in the area. Direct observations and analyses of fecal samples over several years and

sites point to the preference of *T. merula* for the fruits of *Crataegus* (as well as of other very abundant species, *Pistacia* being an exception), of *F. hypoleuca* for the fruits of *Cornus* and *Pistacia*, and of *P. caeruleus* for the fruits of *Pistacia* (M. Fuentes, pers. obs.; J. Guitián, pers. comm.).

The relative preference of *T. merula* for *Crataegus* appears to have stemmed from the very low consumption of these fruits by the rest of birds, rather than from an active choice on the part of *T. merula*. The rank order of the different fruits in the diet of *T. merula* was highly correlated with their rank abundance in the study plot. No such correlations were found for the remaining bird species, largely because they so infrequently fed upon the two most abundant fruits: those of *Crataegus* and *Rosa*. These fruits are too large to be swallowed easily by any bird species studied here except *Turdus* spp. (see Tables 1 and 2). Many bird species can feed on large fruits by pecking at them and swallowing small pieces (Herrera 1984a; Foster 1987; Jordano 1987b; Levey 1987a; Snow and Snow 1988). However, this behavior may require more handling time and energy expenditure than gulping fruits whole (Foster 1987; Hegde et al. 1991; Rey 1992). As a consequence, small birds usually prefer small fruits (Herrera 1984a; Pratt and Stiles 1985; Wheelwright 1985; Jordano 1987a, b). The birds of the present study did peck at the fruits of *Arbutus*, *Malus* and sometimes *Rubus*, which are larger than their gape widths (and larger than the fruits of *Crataegus* and *Rosa*). The fruits of *Arbutus* and *Malus* have pulp-to-seed ratios far greater than those of the other species considered here (Table 1, Fig. 3b), so that pecking at them may be more rewarding than for other fruits. The fruits of *Rubus* are actually composites of small drupelets each containing a very small seed, so that size limitations are not so straightforward.

The preferences of *P. caeruleus* for *Pistacia* and of *F. hypoleuca* for *Cornus* appear to be related to the digestive physiology of the birds and the pulp composition of the fruits. The lipid contents of the pulp of *Cornus* and *Pistacia* are by far the highest among the fruits studied here (Table 1, Fig. 3c). Other evidence also points to the strong preference of European tits (Paridae) for lipid-rich fruits when they feed on fruit pulp (but see Obeso 1985). The fruits of *Euonymus europaeus* [which have 36% of lipids (dry mass) in the pulp], and less so those of *Cornus sanguinea*, seemed to be highly favored by all the *Parus* spp. that ever fed on fruit pulp, and also by *Aegithalos caudatus*, in two English localities (Sorensen 1981; Snow and Snow 1988). *Parus* spp. are also very frequent consumers of *Pistacia terebinthus* fruits in the Sierra de Cazorla, southeastern Spain (Traveset 1993), but not of other fruits in the area (Herrera and Jordano 1981; Herrera 1984a; Obeso 1985). The only fruit remains found in the few droppings available for *Parus major* and *P. ater* in the present study were also of *Pistacia*. Some other evidence is also available for *F. hypoleuca*: the only fruits recorded in its diet in southern France were those of *Pistacia terebinthus*, *Cornus sanguinea* and *Sam-*

bucus nigra (out of 45 species recorded for all bird species; Debussche and Isenmann 1989).

For their part, relative to the rest of fruit-eating bird species, *P. caeruleus* and *F. hypoleuca* included high proportions of insects and/or seeds in their diets, ate few species of fruit and had slow food passage rates through the digestive tract (FPR) (within the range of those of insectivorous and granivorous birds; Table 2, Fig. 2). The birds that eat mainly fruits usually have higher FPR values than those that eat mainly insects and/or seeds (Herrera 1984b; Jordano 1987a; Castro et al. 1989; Karasov 1990; this study; see also Emmons 1991 for mammals). American robins (*Turdus migratorius*) reduce their FPR when switched from a frugivorous to an insectivorous diet (Levey and Karasov 1992). High FPRs are suitable both for processing simple sugars at the concentrations typical of most fleshy fruits and for getting rid of the seed ballast (Herrera 1984b; Martínez del Rio and Karasov 1989; Worthington 1989; Karasov and Levey 1990; Levey and Grajal 1991). Lipids probably need more time to be assimilated than simple sugars, as they must be hydrolyzed and emulsified before being transported through the intestine walls (Mateos et al. 1982; Levey and Grajal 1991; Bosque and Parra 1992; Place and Stiles 1992). The oilbird (*Steatornis caripensis*) feeds almost exclusively on lipid-rich fruits and has food retention times much longer than those of the avian frugivores studied so far (Bosque and Parra 1992). There is also evidence that some frugivorous birds process lipid-poor fruits more rapidly than lipid-rich ones (Holthuijzen and Adkisson 1984; Borowicz 1988). Thus, the relatively low FPRs of insectivorous and granivorous birds may allow (or constrain) them to feed more intensively on lipid-rich pulp. This seems to be the case of *F. hypoleuca* and *P. caeruleus*.

It has been proposed that lipid-rich fruits have evolved to attract a few, highly frugivorous, specialist bird species thought to be efficient dispersers (McKey 1975; Howe and Estabrook 1977; Snow 1981). In Europe, the bird species that show a stronger preference for the most lipid-rich fruits are only moderately frugivorous, and some are also very poor dispersers. Thus, *Parus* spp. feed on the fruits of *Cornus*, *Euonymus* and *Pistacia* by piercing the pulp, usually dropping the seeds under the parent plant or in its immediate surroundings (Snow and Snow 1988; Traveset 1993; pers. obs.). Several authors had previously argued that we should not expect correlations between seed-dispersing efficiency of birds and their patterns of fruit choice or dependence on fruits (Wheelwright and Orians 1982; Pratt and Stiles 1983; Davidar 1987; Levey 1987a; Wheelwright 1988; Reid 1989).

Appendix List of bird species and average number of mist net captures per day, in half-month periods. (*n* is the total number of captures)

	n	Jul1	Jul2	Aug1	Aug2	Sep1	Sep2	Oct1	Oct2	Nov1	Nov2	Dec2
Aegithalos caudatus	33	2.0		1.0	1.5	0.8	0.6		3.0		0.5	0.5
Carduelis carduelis	1	0.2										
C. chloris	5			1.7								
Certhia brachydactyla	4					0.3	0.4	0.3				
Erithacus rubecula	199	2.2	4.0	4.0	7.3	7.5	10.8	9.8	1.5	3.5	2.5	0.5
Ficedula hypoleuca	20				0.8	3.0	1.0					
Fringilla coelebs	9	0.2	0.5	1.0			0.2	0.3	0.5		0.5	
Garrulus glandarius	1						0.2					
Hippolais polyglotta	4	0.2			0.5	0.3						
Luscinia megarhynchos	11	0.2		0.3	1.8	0.3	0.3					
Parus ater	1							0.2				
P. caeruleus	60	2.2	0.5	0.7	3.8	0.8	1.8	2.5	3.0	1.0	0.5	
P. major	17	1.2	0.5			0.8	0.2	0.3	1.0	1.5		
Phylloscopus bonelli	5	0.6	0.5		0.3							
P. collybita	40	2.2	2.5	2.3	2.8	0.8	0.2		1.0			
P. trochilus	17				0.5	2.8	0.8					
Phylloscopus sp.	1				0.3							
Prunella modularis	25	0.6	0.5	0.3	1.8	1.5	0.6	0.5	0.5		0.5	
Pyrrhula pyrrhula	42	1.2	0.5	5.3	1.0		1.4	1.0	1.0	0.5	0.5	
Regulus ignicapillus	40	1.0	1.0	1.7	3.0	1.8	0.6	1.3	0.5			
Sylvia atricapilla	152	3.0	5.5	11.7	1.0	2.0	6.2	7.8	5.5	1.0		2.0
S. borin	24				2.8	2.3	0.8					
S. cantillans	52	2.6	3.0	4.0	3.3	1.8	0.2					
S. communis	3				0.8							
S. hortensis	1					0.3						
S. undata	1						0.3					
Sylvia sp.	1	0.2										
Troglodytes troglodytes	10	0.2	0.5	0.7	0.3	0.3	0.2	0.3	0.5		0.5	
Turdus merula	43	0.4	0.5	1.7	0.8	1.8	1.4	1.5	1.5	2.5	1.5	0.5
T. philomelos	7							1.3	0.5	0.5		
Total	829	20.4	20.0	36.3	33.5	28.8	28.0	26.8	20.0	10.5	7.0	3.5

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