

The role of fruit diet within a temperate breeding bird community in southern Spain

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*In southern temperate regions many fleshy-fruited plant species ripen their fruits during the breeding or early post-breeding season and these are consumed by resident birds. I studied the frugivore community of the summer-fruited tree *Frangula alnus* ssp. *baetica* in southern Spain and the significance of fruit in the diet of adult and recently fledged birds. Twelve species consumed *F. alnus* fruits. Almost 97% of the foraging visits were carried out by the four most abundant species, Robin *Erithacus rubecula*, Blackcap *Sylvia atricapilla*, Blackbird *Turdus merula* and Blue Tit *Parus caeruleus*. During the ripening season Robins and Blackcaps concentrated at fruit-rich sites. Entire families of Blackcap and Blackbird regularly entered fruiting trees together. In contrast, adult Robins always foraged solitarily, and accounted for only 4% of the tree visits, while 96% were realized by recently fledged birds of the first brood. In all species, young birds foraged as efficiently as adults. *F. alnus* fruits are not part of the regular nestling diet, but they are a significant part of the diet for recently fledged Robins during their postnatal dispersal. Conversely, these are the most important and effective seed dispersers while adult Robins scarcely take part in the dispersal of *F. alnus* seeds.*

During recent decades much attention has been paid to the interactions between temperate fleshy-fruited plants and frugivorous birds (Howe & Smallwood 1982, Herrera 1995). A number of field studies and anecdotal reports demonstrate the significance of fruit diet for many European and North American bird species (Willson 1986, Jordano 1992). While fruit-eating in migrating and wintering temperate birds has been extensively studied (Bairlein & Gwinner 1994, Herrera 1995), much less attention has been paid to its role during the breeding period (Breitwisch *et al.* 1984, Snow & Snow 1988, Widmer 1996, Norment & Fuller 1997, Vega-Rivera *et al.* 1998). This is surprising particularly in southern temperate latitudes, where many fleshy fruits mature

during the summer months: Debussche *et al.* (1987) cite 25 summer-fruited species for a region in southern France, and Herrera (1982) gives the same number for two sites in southern Spain.

Breeding frugivores usually move within a constant, well-known territory where fruiting trees are a large, predictable and easily accessible food source. Consequently, fruits may be systematically used by adults to feed nestlings (Breitwisch *et al.* 1984, Bosque & de Parra 1992, Widmer 1996). Furthermore, the easily accessible fruits may be a significant food source for presumably inexperienced young birds during their post-fledging dispersal (Snow & Snow 1988, Boddy 1991, Desrochers 1992, Widmer 1996). The present study describes the frugivore assemblage of the summer-fruited tree *F. alnus* in southern Spain and the role of fruit diet for its members. Since almost all migrant frugivores arrive in the region from September onwards (Finlayson

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1992), it may be expected that *F. alnus* fruits are mostly consumed by the local breeding bird community.

STUDY AREA AND METHODS

The study was conducted from June to September 1997 in the Aljibe, Medio and Puerto Oscuro Valleys of the Aljibe Mountain area, some 40 km northwest of Gibraltar (36°30'N, 5°35'W, Cádiz province, Spain). The small, narrow valleys contain creeks that are active virtually year-round, with dense, usually 10–30 m wide gallery forests. These are dominated by *Alnus glutinosa*, *Frangula alnus* and *Rhododendron ponticum* and surrounded by dense Mediterranean sclerophyllous scrub or light oak (*Quercus suber* and *Q. canariensis*) forests (Ibarra 1993). The reproductive biology of South Iberian *F. alnus* populations has been described in detail by Medán (1994) and Hampe & Bairlein (2000a). The species produces blackish, glossy drupes (diameter 9.0 ± 0.8 mm, fresh weight 402 ± 97 mg (mean \pm sd); $n = 100$). The water content of the pulp is about 83%, the soluble carbohydrate content averages 51% dry weight. In 1997 about 95% of the fruit crops ripened between 24 June and 28 August. During most of this period, only two other fleshy-fruited species, the vines *Rubus ulmifolius* and *Smilax aspera*, matured appreciable numbers of fruits in the study area. Additionally, some *Phillyrea angustifolia* shrubs started fruiting in the first half of August (pers. obs.).

Between 3 June and 7 September 1997 I assessed the frugivorous avifauna of the study area using a point-count method (Bibby *et al.* 1992). Twenty counts were performed at five-day intervals. During each census birds were recorded at 15 points, five of them located at sites with high and ten at sites with low abundance of *F. alnus* fruits. (Fruit abundance was determined according to the number and size of fruiting *F. alnus* trees visible from the count point; ranging between zero trees and eight trees bearing about 50 000 fruits.) Counts started about sunrise and lasted five minutes per point. Birds observed within a radius of 50 m were recorded and assigned to either the *F. alnus* habitat (gallery forest, covering 35% of the censused area) or other habitats (sclerophyllous scrub or oak forest, covering 65%).

Between 8 July and 16 August I observed

eight fruiting *F. alnus* trees during a total of 54 hours. Observations were carried out in three- to four-hour sampling frames and were spread across the ripening season (for more details see Hampe & Bairlein 2000b). During foraging visits, i.e. the arrival of a bird followed by observable fruit foraging activity, I recorded the following details of birds whenever possible: (1) species, (2) age (adult or first-summer), (3) duration of the visit, (4) number of fruits ingested, (5) technique used for ingesting fruits (perched or leaping/flying, see Snow & Snow 1988), and (6) success of the ingestion attempt. In addition to the birds recorded during the systematic tree observations, I included foraging records made in the study area in all analyses that did not refer to visit rates. Based on the observations, the function of bird species for the dispersal of *F. alnus* seeds was determined according to the definitions by Jordano (1995).

The calculations of seasonal trends in frugivore abundance and tree visit rates were based on the point-count dates. The rate of foraging visits was significantly affected by the respective crop size of the observed tree (ranging between 3200 and 17 000 fruits; $r = 0.87$, $F = 17.78$, $df = 7$, $P < 0.01$). Therefore I included the crop size in the analysis and carried out a multiple linear regression considering the crop size and the date of the ripening season as independent variables and the number of foraging visits per hour as the dependent variable. If not otherwise stated, means \pm 1 sd are given throughout the paper.

RESULTS

Frugivorous community

A total of 38 bird species was recorded of which 12 were observed consuming *F. alnus* fruits. These 12 species accounted for a total of 1273 point count records and 528 foraging visits. Seven species acted as seed dispersers, three consumed fruits without dispersing seeds, and two occasionally dispersed seeds of the fruits they consumed (Table 1). All species breed in the study area except the scarce migrant Garden Warbler *Sylvia borin*. The frequency of tree visits by single species was significantly correlated with their abundance in the study area (Fig. 1, Spearman's rank: $r_s = 0.75$, $n = 12$, $P = 0.005$). Over 83% of the point count records

Table 1. Foraging visits and habitat preferences of bird species consuming *F. alnus* fruits.

	Foraging visits	Type of frugivory ^a	Point count records	% <i>F. alnus</i> habitat ^b	% other habitats ^b	<i>P</i> ^c
Great Spotted Woodpecker <i>Dendrocopus major</i>	1	SC	6	0	100	–
Robin <i>Erithacus rubecula</i>	254	SD	572	59	41	***
Chaffinch <i>Fringilla coelebs</i>	1	SC	60	7	93	***
Jay <i>Garrulus glandarius</i>	1	SD	10	40	60	–
Spotted Flycatcher <i>Muscicapa striata</i>	3	SD	17	29	71	–
Blue Tit <i>Parus caeruleus</i>	61	PCSD ^d	152	39	61	ns
Great Tit <i>Parus major</i>	2	PC	72	17	83	**
Nuthatch <i>Sitta europaea</i>	4	SCSD ^d	39	3	97	***
Blackcap <i>Sylvia atricapilla</i>	122	SD	213	72	28	***
Garden Warbler <i>Sylvia borin</i>	1	SD	2	50	50	–
Blackbird <i>Turdus merula</i>	74	SD	125	52	48	***
Mistle Thrush <i>Turdus viscivorus</i>	4	SD	5	0	100	–

^aSD, seed disperser; SC, seed consumer; PC, pulp consumer (according to Jordano 1995).

^bCover 35% (*F. alnus* habitat) and 65% (other habitats), see methods.

^c χ^2 -test: ** $P < 0.01$; *** $P < 0.001$; ns, not significant; –, not tested.

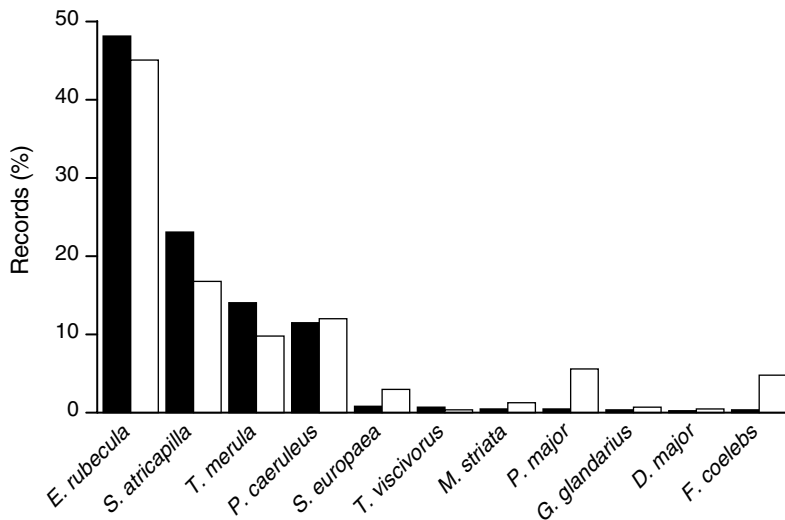
^dEntire fruits were occasionally carried away by *Parus caeruleus* (five of 61 records) and *Sitta europaea* (one of four records).

and 96% of the foraging visits included Robin *Erithacus rubecula*, Blackcap *Sylvia atricapilla*, Blackbird *Turdus merula*, and Blue Tit *Parus caeruleus* (Table 1).

Temporal and spatial patterns of frugivore occurrence

The abundance of frugivores in the study area remained constant throughout the study period

(Fig. 2, Kolmogorov–Smirnov: $Z = 1.22$, $n = 20$, $P = 0.10$) and varied only in the Blue Tit ($Z = 1.57$, $n = 20$, $P = 0.01$; for all other species $P > 0.05$). In contrast, the overall rate of tree visits declined continuously throughout the ripening season (Fig. 2, $r = -0.91$, $n = 8$, $P = 0.01$), although among the four most important frugivorous species the Blackcap was the only species showing a significant decrease when tested alone ($r = -0.88$, $P = 0.02$).

**Figure 1.** Presence in the study area (□) and foraging visits (■) of the bird species observed consuming *F. alnus* fruits.

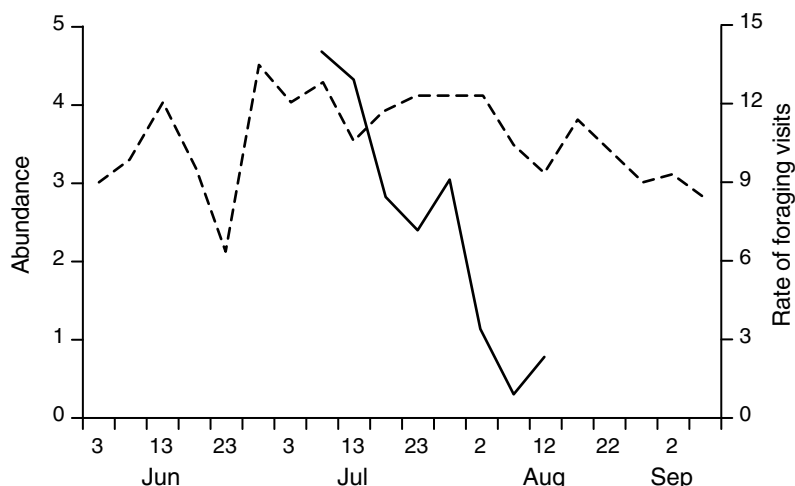


Figure 2. Abundance of the frugivorous community in the study area (---) and rate of foraging visits (—) during the study period. Abundance is expressed as records/count point and the visit rate was calculated by a multiple regression considering point-count date and crop size of the observed tree as independent variables and the number of foraging visits per hour (all species combined) as dependent variable.

Robin, Blackcap and Blackbird preferably used the habitat of *F. alnus* (Table 1). Their preference remained constant throughout the ripening season (Kolmogorov–Smirnov: $Z \leq 0.93$, $n = 8-20$, $P > 0.05$ for all species; all censuses with less than eight records per species were omitted). In contrast, the Blue Tit did not show preferences for the *F. alnus* habitat (Table 1).

Over the whole study period 5.2 ± 1.7 birds were observed per count at sites rich in fruits but only 3.8 ± 0.6 at points with scarce fruit abundance ($t = 3.5$, $n = 40$, $P = 0.002$). During the ripening season more Robins and Blackcaps occurred at fruit-rich points than before and afterwards ($\chi^2_{\text{Blackcap}} = 12.3$, $df = 1$, $n = 213$, $P < 0.01$; $\chi^2_{\text{Robin}} = 5.1$, $df = 1$, $n = 572$, $P < 0.05$). In contrast Blackbird and Blue Tit did not concentrate at fruit-rich points when ripe fruits were available.

Ratio, association and behaviour of adult and recently fledged frugivores

Recently fledged birds dominated foraging visits in the three most important species (Fig. 3). (In contrast to the 'regular' seed disperser species, Blue Tits were not systematically distinguished by age.) The percentage of young birds was considerably higher in Robin than in

Blackbird and Blackcap (Fig. 3; $\chi^2 = 70.30$, $df = 2$, $n = 379$, $P < 0.001$).

Most Robins entered the trees solitarily (Table 2). Young birds foraged together, while associations among adults or between adults and young were never recorded. In contrast, adult Blackcaps and Blackbirds regularly foraged together with young birds, most likely their recently fledged offspring. Consequently,

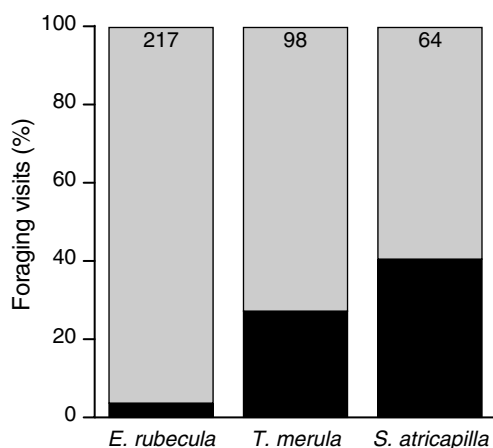


Figure 3. Percentage of foraging visits realized by adult (black) and recently fledged (tinted) birds of the three most prominent species; numbers in columns represent the numbers of foraging visits.

Table 2. Association of recently fledged and adult foraging birds with other individuals.

Associated with (%)	Robin		Blackcap		Blackbird	
	Post-fledging	Adult	Post-fledging	Adult	Post-fledging	Adult
Recently fledged conspecifics	16.7	0	12.1	5.0	31.9	0
Adult conspecifics	0	0	3.4	10.0	0	0
Recently fledged and adult conspecifics	0	0	12.1	15.0	12.8	23.5
Conspecifics of unknown age	2.9	0	13.8	2.5	17.0	0
Other species	6.2	0	6.9	10.0	12.8	23.5
No other bird	73.8	100	51.7	57.5	25.5	53.0
No. foraging visits	209	8	58	40	47	17

individuals of both species foraged considerably more often in association with conspecifics than did Robins (Table 2; $\chi^2 = 36.37$, $df = 2$, $n = 379$, $P < 0.001$). The percentage of assemblages with other bird species did not differ among the three species ($\chi^2 = 6.11$, $df = 2$, $n = 379$, $P > 0.05$).

A comparison of the foraging behaviour showed that recently fledged birds of all three species foraged as efficiently as adults and did not fail more often in removing fruits (Table 3).

DISCUSSION

The role of fruit diet within the breeding bird community

Southern Spanish *F. alnus* fruits are consumed by several species of the local breeding bird community. Nevertheless, many of them either eat fruits irregularly or are not abundant in the study area. Only four species make regular use of the food source. Two of them, Blackbird and Blue Tit, appear to act as opportunists as they do not change their spatial pattern of activity during the ripening season. Furthermore, Blue Tits occur mainly outside the riparian vegetation, the habitat of *F. alnus*. In contrast, the other two species, Blackcap and Robin, preferably move within the gallery forests and concentrate at fruit-rich sites when ripe fruits become available. In this study they appear to rely most heavily on fruit diet during the breeding and early post-breeding period. The almost year-round high degree of frugivory in the Blackcap has been described several times (Berthold 1976, Jordano & Herrera 1981, Herrera 1984, Jordano 1995). The

decline in Blackcap visits during the study may be due to an increasing availability of other fruits, as the abundance of *F. alnus* fruits tends to decline during its ripening season. The importance of summer frugivory in Robin and Blackbird appears to vary among populations, while both rely heavily on fruit diet during autumn and winter (Berthold 1976, Herrera 1981, 1984, Debussche & Isenmann 1985, Snow & Snow 1988, Boddy 1991, Jordano 1995). Fruit consumption is generally least significant in the Blue Tit, although the species regularly includes seeds or pulp of fleshy fruits in its diet (Herrera 1984, Jordano 1995). Interestingly, Blue Tits do not consume fruits in Central European *F. alnus* populations (Hampe & Bairlein 2000b). In southern Spain they may use them as a water source during the hot and dry summer months rather than for nutrients (Berthold 1976, Jordano 1995).

Frugivorous behaviour of adult and recently fledged birds

During the breeding season fleshy fruits may play a significant role in the nutrition of nestlings although, with a few exceptions (e.g. Breitwisch *et al.* 1984, Widmer 1996), they seem to be an emergency diet during periods of low invertebrate availability (Berthold 1976, 1984, Snow & Snow 1988). In the present study, the percentage of recently fledged Blackcaps observed may reflect the chicks of the first brood, while in Blackbirds the proportion of young birds is rather higher, and in the Robin it largely exceeds values that may be expected even in years of extremely high reproductive success (Cramp & Simmons 1988–92, Glutz von

Table 3. Foraging behaviour of recently fledged and adult individuals. *n* is given in parentheses.

	Robin		Blackcap		Blackbird	
	Recently fledged	Adult	Recently fledged	Adult	Recently fledged	Adult
No. foraging visits	209	8	58	40	47	17
Duration (s)	29	33	44	56	161	142.5
Median time	199	7	43	37	40	12
Fruits ingested	1.2 ± 0.4 (178)	1.2 ± 0.4 (5)	1.8 ± 0.8 (29)	1.8 ± 0.6 (26)	5.8 ± 3.9 (12)	4.0 ± 0.8 (4)
Fruits ingested/min	3.5 ± 5.2 (175)	2.9 ± 2.1 (5)	2.6 ± 1.3 (29)	2.4 ± 1.8 (26)	2.3 ± 1.4 (12)	4.4 ± 0.7 (4)
Successful ingestion attempts (%)	87.3 (236)	85.7 (7)	92.7 (55)	94.2 (52)	85.7 (70)	100 (16)
Ingestion technique						
perched (%)	22.9	14.3	87.5	89.3	86.4	75
in flight (%)	77.1 (179)	85.7 (7)	12.5 (32)	10.7 (28)	13.6 (22)	25

Median test, Mann–Whitney U-test or χ^2 -test: $P > 0.05$ in all cases.

Blotzheim & Bauer 1988–97). These observations clearly support the hypothesis that the easily accessible *F. alnus* fruits are important for the nutrition of recently fledged birds of the first brood (Sullivan 1989, Desrochers 1992). To date there has been little empirical evidence to support this hypothesis (Snow & Snow 1988, Vega-Rivera *et al.* 1998). In contrast, adult Robins rarely consume *F. alnus* fruits. The different behaviour of adult and young Robins may explain why observations of summer frugivory are conflicting in this species: in areas or years of low reproduction frugivorous behaviour may be recorded infrequently.

While in the Robin foraging visits only of solitary birds or small groups of young were observed, fruiting trees were regularly frequented by entire families of Blackcap and Blackbird. These birds appear to concentrate and remain at large trees within their breeding territory as soon as the young have left the nest (pers. obs., Snow & Snow 1988). In contrast, recently fledged fruit-eating Robins appear to be more mobile. In an extreme case, 16 tree visits of young Robins recorded within a three-hour sampling frame were carried out by at least eight different individuals. (Individuals could be distinguished based on plumage differences during their post-juvenile moult.) This observation suggests that most were birds on their post-fledging dispersal (see also Berthold *et al.* 1991), which do not stay a long

time near the same tree. This behaviour may lower the risk of being detected and attacked by territorial adults (Cramp & Simmons 1988–92).

In contrast to Boddy (1991), my data did not show any effects of bird experience on the foraging behaviour of adult and recently fledged individuals. Young birds neither forage less efficiently nor fail more often in ingesting fruits than adults, supporting the notion that fleshy fruits are an easily obtainable energy source for foraging birds regardless of their experience. This holds true even for Robins, which often have to leap or make short flights to tear off fruit (Snow & Snow 1988), and contrasts with other studies which have documented clear relationships between bird experience and foraging success (Desrochers 1992, Smith & Metcalfe 1994).

The role of different frugivores for the seed dispersal of *F. alnus*

Primary seed dispersal of southern Spanish *F. alnus* populations is virtually maintained by Robin, Blackcap and Blackbird. All preferably move within the gallery forest, the plant's habitat. Nevertheless, the small home-range of Blackcap and Blackbird families foraging on *F. alnus* fruits leads to the deposition of many seeds beneath the parent plant (Hampe, unpubl. data). The presumably non-territorial

(Cramp & Simmons 1988–1992) young Robins appear to move more and further (Johnstone 1998, see also observation described above), and thus disperse seeds over larger distances. Additionally, they remove the largest seed quantity. Consequently, they must be considered the most important and effective dispersers of *F. alnus* seeds. In contrast, adult Robins scarcely contribute to the seed dispersal of *F. alnus*. To my knowledge, this study reveals for the first time that different age classes of the same bird species may vary in their significance for the seed dispersal of a plant species. Although this difference certainly has no co-evolutionary significance (Herrera 1995, 1998), it may have important ecological consequences for the plant's recruitment, e.g. if adult and young Robins tend to deposit seeds in different microhabitats that vary in their seed predation or seedling survival rate (Herrera *et al.* 1994).

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