

Blackcaps, *Sylvia atricapilla* and blackbirds, *Turdus merula* feeding their nestlings and fledglings on fleshy fruit

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Received 3 June 2004; Accepted 22 November 2005

A b s t r a c t. There is very little information on the importance of fleshy fruit in the diet of the nestlings and fledglings of partially frugivorous Holarctic passerines. In an area of 0.6 km² in northwestern Spain, it was verified during 2001–2003 that at least one blackcap *Sylvia atricapilla* pair and five blackbird *Turdus merula* pairs fed their offspring on a certain proportion of ivy *Hedera helix* fruit. Observations made on a blackcap nest in May showed that the parents fed older nestlings on animal prey on 60.7% of occasions and 39.3% on fruit (n = 140 total number of identified feeds). The female fed nestlings on fruit more often than the male. According to observations carried out on five ivy plants in May, blackcaps brought fruit in their bills to feed nestlings or fledglings on 40.3% of 67 feeding visits and blackbirds on at least 22.1% of 86 feeding visits. The blackcaps consistently carried one fruit and the blackbirds between three and five. Both species fed their young on fruit under very different meteorological conditions. Seeds found in the faecal sacs of their nestlings showed high potential germination viability (95.6% undamaged seeds and 4.4% cracked seeds; n = 46 total seeds except for those gnawed by rodents), so the adults probably acted as indirect vectors in dispersing ivy whilst carrying faecal sacs away from the nest.

Key words: passerines, frugivory, nestling diet, fledgling diet, Spain

Introduction

Most bird species have high nutrient requirements for growth, so fleshy fruit, which is low in protein, has traditionally been considered as inadequate food for nestlings (reviews by Snow & Snow 1988, Ricklefs et al. 1998), though a few neotropical species are particularly well adapted to feeding them on fruit alone (Bosque & Parra 1992 and references given by these authors). Several partially frugivorous Holarctic species include fruit in their nestling and fledgling diets but very little research has been carried out and there are few quantitative and qualitative studies on the subject. The information available tends to qualify fruit as a secondary food or as an emergency food during bad weather when there is no animal prey (Glutz von Blotzheim 1973, Berthold 1976a, 1977, 1984), with the exception of work by Breitwisch et al. (1984) on the northern mockingbird *Mimus polyglottos* and Gutiérrez et al. (2001) on the black redstart *Phoenicurus ochruros*. These authors observed consistent feeding on fruit, which increased at the end of the period in the nest and during the fledgling stage before the young became independent. According to Breitwisch et al. (1984) arthropods, which are rich in protein, contribute to rapid structural growth in nestlings during the first days of life, whereas fruit, which is rich in carbohydrates, provides enough energy to maintain body temperature when endothermy is acquired. Also, fleshy fruit is usually a very important part of the diet of independent young Holarctic frugivorous birds (Boddy 1991, Vega-Rivera et al. 1998, Hernández 2000, Hampe 2001).

The aim of this paper is to widen knowledge on frugivory in nestlings and fledglings of blackcaps *Sylvia atricapilla* and blackbirds *Turdus merula*, through data obtained in north-western Spain on a) the proportion of fruit brought by the parents to the nest during the day in comparison with animal prey, b) the role of males and females in bringing fruit, c) the number of fruits brought for each feed, d) feeding offspring on fruit under different meteorological conditions, e) fleshy fruit seeds in the faecal sacs of nestlings and their potential dispersion viability, and f) the degree of temporal coincidence between breeding in these species and availability of ripe fruit. All data on frugivory refer to ivy *Hedera helix*.

Material and Methods

The study area covers 0.6 km² and is situated in the Torío river valley, between Ruiforco and Manzaneda (30TTN93 U.T.M. coordinates, 900 m a.s.l., León province, NW Spain). It is part of the Supramediterranean bioclimatic stage in the Mediterranean biogeographical region, but is very near the Eurosiberian region. The landscape is a mosaic of riparian woodland, hedgerows, and irrigated pastureland. The most common species in these hedges are hazel *Corylus avellana*, dog rose *Rosa canina*, blackberry *Rubus ulmifolius* and blackthorn *Prunus spinosa*. Ivy has a frequency of appearance of 8% in 4 m long hedge samples (Hernández & Alegre 1991).

During 2001–2003 signs of a partially frugivorous diet in the nestlings and fledglings of blackcaps and blackbirds were observed, consisting mainly of adults with ivy fruit in their bills in the proximity of the nest or carrying fruit from ivy plants in their bills. Sampling was later carried out to record quantitative data. The signs and samplings were as follows:

Blackcaps bringing food to the nest

On 6th May 2001 I discovered a blackcap nest in a dog rose, blackberry and blackthorn hedge, at a height of 0.9 m from the ground. The female was in the nest. On 13th May, and under sunny weather conditions, I saw the female near the nest with an ivy fruit in her bill, ready to feed. On 16th May the nest contained three large well-fledged nestlings and with the aid of binoculars and a terrestrial telescope, and camouflaged amongst vegetation at a distance of 20 m, I watched the parents bringing food for 8 h, 4 h in the morning (07:00–11:00 h, solar time) and 4 h in the afternoon (13:00–17:00 h, solar time). I recorded each feed and differentiated between fruit and animal prey, as well as the number of fruits brought each time and the sex of the adult carrier. The parents generally perched on branches in the open near the nest before entering to feed. However, they sometimes entered the nest directly and it was not possible to identify the type of food brought. Outside the observation time I verified that the ivy fruit was mostly taken from two plants growing on two black poplars *Populus nigra*, standing next to each other in a hedge 65 m from the nest. During the observation period it rained heavily for 50 min, moderately for 3 h, lightly for 2 h 25 min and it did not rain for 1 h 45 min; the temperature was cool and remained below 12 °C.

Blackcaps bringing fruit from ivy plants to feed their fledglings

On 18th May 2001, the nestlings had already left the previously mentioned nest and I observed the family group in a hedge 35 m in the direction of the previously mentioned ivy plants. On

19th and 20th May the group was in a hedge at a distance of between 60 and 75 m from the nest, very close to these two ivy plants. After verifying several times that the parents picked fruit and brought it in their bills to feed the fledglings, I spent a total of 4 h recording the number of times the blackcaps visited the ivy plants (2 h in the afternoon, 16:00–18:00 h, on 19th May; 2 h in the morning, 08:00–10:00 h, on 20th May; solar time), hidden amongst vegetation at a distance of 20 m and using binoculars. I differentiated between feeding visits with and without bringing fruit. In the former case, the birds usually ate fruit, swallowing it immediately before loading their bills with food for their fledglings. I recorded the number of fruits per load and the sex of the carrier. The ivy plants were not only visited by the parents in this group but also by at least one other pair taking turns to incubate a nest of four eggs situated at a distance of 45 m. All the collecting visits were presumably made by the pair feeding fledglings. Feeding visits by other frugivorous species were also recorded but were probably underestimated due to the monitoring of the blackcaps and also because larger species rarely visit the plants with the observer at such a short distance. Both sampling days were sunny with maximum temperatures of 20 °C.

Analysis of the faecal sacs of blackcap nestlings

On 16th May 2001, whilst recording blackcaps delivering food to their nestlings, I observed that after feeding, the adults frequently left the nest carrying faecal sacs in their bills which they placed on the branches of trees and shrubs at distances of 2–25 m. On the same day and outside the observation period I collected 12 of these sacs. Their contents were analysed to calculate the percentage of frequency of appearance of ivy seeds and arthropods, and undamaged seeds (potentially viable) were differentiated from cracked (non viable) ones. Aborted (flattened and empty) seeds were discarded.

Analysis of the faecal sacs of blackbird nestlings

On 18th April 2003, I found a blackbird nest with three small nestlings on a crack willow *Salix fragilis*, 1 m from the ground. On 19th April I attempted to observe the adults bringing food to the nest, but was unable to find a suitable place to identify the feeds directly. On 26th April the three nestlings were still in the nest and had grown considerably, and on 3rd May they had already left it. Fragmented and flattened remains of the faecal sacs of the nestlings could be seen at the bottom of the nest. These were collected for analysis and to check for undamaged or cracked seeds. It was not possible to quantify the sacs.

Blackbirds bringing fruit from ivy plants to feed offspring

On 16th May 2003, I observed a male blackbird feeding on the fruit of an ivy plant growing on a black poplar tree in a hedge. When he had finished he collected a number of fruits and left the plant to feed his nestlings or fledglings in an unknown place. That day, and on 17th May I spent 5 h recording visits by blackbirds to the ivy plant (always in the evening between 15:00–18:00 h, solar time), hidden amongst the vegetation at a distance of 40 m and using binoculars. I recorded the same data as in blackcaps. After leaving the ivy plant, the blackbirds flew long distances to unknown places. Feeding visits by other frugivorous birds were

probably underestimated due to the monitoring of the blackbirds and also because smaller species could not be seen at that distance of observation. Both sampling days were sunny, with maximum temperatures of 17.5 °C and 20 °C, respectively. On 23rd May I tried to resume sampling but there was hardly any fruit left on the ivy plant and frugivorous birds had stopped visiting it. On the same day I found two ivy plants in a hedge at a distance of almost 1 km growing on two black poplars, situated next to each other and bearing a considerable amount of ripe fruit. On 23rd and 24th May I spent 4 hours recording visits by blackbirds to the ivy plants (always in the evening, between 16:00–18:00, solar time), camouflaged at a distance of 40 m, using binoculars and recording the same data. I was unable to discover where they went to after leaving the plants. On 23rd May it was cloudy but warm with a maximum temperature of 25 °C, and on 24th May it was sunny but the temperature dropped sharply and remained below 14 °C. Due to the distance between the two observation points I assumed that the birds observed on 16th and 17th May were different to those observed on the 23rd and 24th of May.

During 2001–2003 I obtained data, but not systematically, on the phenology and biology of breeding in blackcaps and blackbirds. I found five nests occupied by blackcaps and seven by blackbirds, and recorded each time the birds fed fledglings or were seen carrying food in their bills. In May 2003 I collected four lots of ivy fruit, each consisting of 30 units and belonging to different plants, to measure the maximum width and length of the fruit and to count the number of seeds per fruit, discarding the aborted ones. During 2001–2003 I obtained data on the fruiting season of the ivy and on other plant species producing fleshy fruit, at maximum intervals of two weeks.

The statistical analyses followed F o w l e r et al. (1998) and included the chi-square test (χ^2) (with Yates correction for 1 degree of freedom), Mann-Whitney U-test, and ANOVA (F). $P < 0.05$ was accepted as statistically significant. In the calculated means the measure of variability was the standard deviation (SD). Some results are given qualitatively when the sample size was too small.

Results

Blackcaps bringing food to the nest

During the 8 h observation time the blackcaps fed their nestlings 164 times (3.4 feeds/10 min). The male fed 81 times and the female 83, which is not significantly different to an expected 1:1 ratio (82:82) ($\chi^2_1 = 0.006$, ns). The collected food was identified on 140 occasions: 85 times (60.7%) animal prey and 55 times (39.3%) ivy fruit. All the animal prey, both adult and larvae, appeared to be arthropods. The birds usually carried more than one prey in each load, though this was not quantified. However, they consistently carried a single fruit in each load. No arthropod-fruit mixed feeds were observed.

The number of feeds for each one-hour interval is shown in Fig. 1. There was an apparent slight decline half way through the day, which was not significantly different to an expected 1:1 ratio (164 feeds/8 hours = 20.5 feeds per hour) ($\chi^2_7 = 4.48$, ns), that is, the feed rate was constant throughout the day. There was no significant association between the number of feeds by each sex and the time of day ($\chi^2_7 = 4.84$, ns), or between the type of food brought (arthropods/fruit) and the time of day ($\chi^2_7 = 7.15$, ns, considering the 140 identified feeds). A significant association was observed between the sex and type of food loaded ($\chi^2_1 = 10.15$, $P < 0.005$, considering the 140 identified feeds). The male brought more arthropods (74.0% of

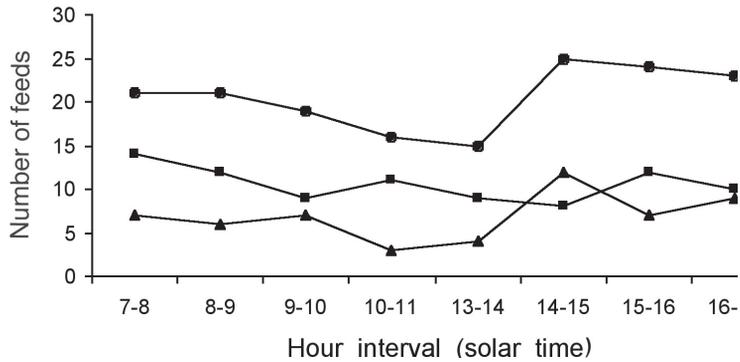


Fig. 1. Frequency of feeds to nestlings aged approximately 10 days in a blackcap *Sylvia atricapilla* nest during the day (8 h observation, 16th May 2001, northwestern Spain; three nestlings in the nest). Circles: total number of feeds (n = 164). Squares: feed identified as animal prey (n = 85). Triangles: feed identified as ivy *Hederia helix* fruit (n = 55). 24 feeds were not identified.

73 feeds) and the female more fruits (53.7% of 67 feeds). Out of the total number of 55 fruits brought to the nest, the female carried 36 (65.5%) and the male 19 (34.5%).

Blackcaps bringing fruit from ivy plants to feed their fledglings

During the 4 h sampling period 83 feeding visits by frugivorous birds were recorded: 67 (80.7%) by blackcaps, 13 (15.7%) by garden warblers *Sylvia borin* and 3 (3.6%) by blackbirds. Attacks among blackcaps of different pairs and by blackcaps on garden warblers whilst feeding on the ivy plants were recorded. The blackcaps visited the plants 40 times (59.7%) to feed without collecting and 27 times (40.3%) to collect fruit for their fledglings. Only one fruit was transported during each visit. The female collected 16 fruits (59.0%) and the male 11 (41.0%), maintaining the important role of the female in this aspect as there was no significant difference between the stage of nestlings and fledglings in the number of fruits brought by either sex ($\chi^2_1 = 0.08$, ns), assuming that all the fruit taken to the fledglings was from the observed ivy plants.

Analysis of the faecal sacs of blackcap nestlings

Arthropods and ivy seeds appeared in 100% and 91.7%, respectively, of the faecal sacs analysed (n = 12). Amongst the arthropods, hymenopterans (mainly ants) and coleoptera were most common, both with 100% frequency of appearance, followed by lepidopteran larvae (58.3%) and spiders (41.7%), and to a lesser extent, orthopterans and dipterans (25.0% in both cases). Remains of snails were also found in one sac. Twenty ivy seeds (1.8 seeds/faecal sac, considering the 11 faecal sacs containing seeds) were found, 18 of which were undamaged (90%) and 2 cracked (10%).

Analysis of the faecal sacs of blackbird nestlings

The remains of the faecal sacs collected from the nest mostly contained soil, probably from ingested earthworms, and 41 ivy seeds, 26 intact and 15 gnawed by wood mice *Apodemus sylvaticus*. A small number of elytra from coleopterans were also found.

Blackbirds bringing fruit from ivy plants to feed offspring

During the 9 h observation period, 122 feeding visits by frugivorous birds were recorded: 86 (70.5%) by blackbirds, 26 (21.3%) by woodpigeons *Columba palumbus*, eight (6.6%) by blackcaps and two (1.6%) by song thrushes *Turdus philomelos*. The blackbirds made feeding visits without collecting fruit 29 times (33.7%), they collected fruit to feed their nestlings or fledglings 19 times (22.1%), and a high number of visits (38, 44.2%) were for feeding though it was not possible to ascertain whether fruit was collected or not, so the importance of fruit collection was probably underestimated. The percentages were 27.5%, 42.5% and 30.0%, respectively, for the ivy plant observed on 16th and 17th May (40 visits), and 39.1%, 4.3% and 56.5% for the ivy plants observed on 23rd and 24th May (46 visits). On 12 (63.2%) of the 19 collecting visits, the birds ate first and on the remaining seven it was not possible to ascertain whether they had eaten or not.

The males made 50 visits (58.1%), females 27 (31.4%), and young birds nine (10.5%). The males visited the ivy plants on a significantly higher number of occasions than the females in comparison with an expected 1:1 ratio (38.5:38.5) ($\chi^2_1 = 6.28$, $P < 0.05$), but there was no significant association between sex and type of visit (collecting checked/non collecting checked, 11/14 and 8/6 for males and females respectively) ($\chi^2_1 = 0.20$, ns). At each observation site at least two different pairs visited the ivy plants and collected fruit, as in both cases two specimens of the same sex were seen storing fruit in their bills at the same time. Attacks between birds belonging to different pairs were recorded at both observation sites.

The number of fruits collected was recorded on 15 occasions (4.40 ± 0.63 , range = 3–5; males: 4.38 ± 0.74 , range = 3–5, $n = 8$; females: 4.43 ± 0.53 , range = 4–5, $n = 7$). No significant difference between sexes was observed after medians were considered ($U = 28$, ns). The fruits were always placed inside the bill one by one.

Breeding phenology and biology of blackcaps and blackbirds / Characteristics of ivy fruits / Fruiting season of fleshy fruit plant species

I found nests occupied by blackcaps with eggs or nestlings from the end of April to the beginning of July, the clutch or brood size was 3–4, and both males and females incubated the eggs and fed the nestlings. The blackbirds had eggs or nestlings in their nests from the end of March to the beginning of July, the clutch or brood size was 3–4, the eggs were incubated by the females alone and both males and females fed the nestlings. One nest was presumably used by the same pair for the first and second clutch, both of which were successful and the nestlings hatched in mid April and at the end of May, respectively. In April and at the beginning of May blackbirds carrying food in their bills collected mostly earthworms and other invertebrates such as slugs and insects during the rest of May and in June.

The mean length of the 120 ivy fruits measured was 6.89 ± 0.62 mm (range = 5.2–8.7) and the mean width 7.07 ± 0.91 mm (range = 4.9–8.8); the mean number of seeds was 1.65 ± 0.71 (range = 1–4). No significant differences in the mean number of seeds among the four lots of fruits were observed ($F_{3,116} = 0.60$, ns). However, there were differences in the mean length ($F_{3,116} = 12.07$, $P < 0.001$) and width ($F_{3,116} = 5.16$, $P < 0.005$).

Eighteen species of fleshy fruit plants were found in the study area. The ivy plants displayed considerable quantities of ripe fruit from the beginning of March to the beginning of June. Other ripe fruit available during the breeding period of the blackbirds and blackcaps

included: in March and April dog rose, privet *Ligustrum vulgare* and guelder rose *Viburnum opulus*, though they were very scarce; in May only ivy; in June cherry *Prunus avium*, which was abundant on a few very scattered trees, and a small number of gooseberries *Ribes uva-crispa*; in July, a few cherries, gooseberries, dewberries *Rubus caesius* and woody nightshade *Solanum dulcamara* and white bryony *Bryonia cretica* fruits.

Discussion

Fleshy fruits seem to be a usual part of the diet of the nestlings and fledglings of frugivorous birds in the study area. This supports observations by Snow & Snow (1988) in England on *Turdus* blackbirds and thrushes and *Sylvia* warblers regularly feeding their nestlings on fruit. Quantitatively, the estimated importance of fruit taken to the nest by blackcaps was similar to that found for other Holarctic frugivorous species: 30–35% of loads for nests with older northern mockingbird nestlings (Breitwisch et al. 1984), a mean of 14% (range 7–28% depending on the nests) for black redstart considering nestlings of any age (Gutián et al. 2001, who stated that these percentages increased for grown nestlings and that around 30% of the food taken to fledglings was fleshy fruit). Carbohydrates and lipids obtained from the fruit largely cover the energy requirements for general body maintenance and activity, which increase when endothermy is acquired (Morton 1973, Foster 1978, Breitwisch et al. 1984). Ivy fruit is a good source of energy as it contains 47% carbohydrates and 32% lipids with regard the dry weight of the pulp, and provides just over 5 kcal per gram of dry pulp (Herrera 1987, Snow & Snow 1988).

Although several authors have attributed European frugivorous birds feeding their nestlings and fledglings on fruit to extreme meteorological conditions, these conditions are often disparate (cold, hot, dry, wet weather), and so are the reasons explaining this behaviour (lack of better food, water demand) (Lutz von Blotzheim 1973, Berthold 1984, review by Snow & Snow 1988). In the study area blackcaps and blackbirds collected ivy fruit in both bad (continuous rain, low temperatures) and good (sunshine, normal temperatures for the breeding season) weather. Similar research carried out in Holarctic latitudes did not link fruit collection to determined meteorological conditions (Breitwisch et al. 1984, Snow & Snow 1988, Gutián et al. 2001). So, fleshy fruit alone is almost certainly a profitable food for the nestlings and fledglings of frugivorous species in these latitudes. It is easily obtained and the fruiting season is predictable, making it very attractive as food for offspring in spring and summer (Morton 1973, Breitwisch et al. 1984, Snow & Snow 1988, present study) and also to independent young birds not yet experts in catching animal prey (Feare 1984, Vega-Rivera et al. 1998, Hernández 2000, Hampe 2001).

However, in temperate and Mediterranean regions in the northern hemisphere ripe fleshy fruit is most abundant and diverse outside the breeding period of frugivorous birds, from the onset of summer to mid winter (review by Herrera 2002, pers. obs. for the study area), which is probably the main limiting factor for using this resource during this time. The breeding period of blackcaps and blackbirds in the study area generally coincided with information available on these species in the western Palearctic (Crampton 1988, 1992). In the study area only ivy fruit was produced in abundance during March–May and cherries moderately so during June–July. In some years it is normal for cherry production to be non-existent or very limited due to late frost (pers. obs. for a 18-year series). In a recent study conducted in the same valley during July–August 2005 I spent 30 hours directly observing birds that fed on fruit in 10 cherry trees (in prep.), coinciding with an abundant crop; handling of fruit was

difficult to check due to the thick foliage and the attention was paid to number of feeding visits, but on several occasions the blackbirds loaded their bills with two or three fruits (eight times) and the blackcaps did with a few pieces of pulp (two times); moreover, some great tits *Parus major* and bullfinches *Pyrrhula pyrrhula* fed their fledglings on pulp in the cherry trees (five and nine times respectively); most of these records occurred in early July under sunny and hot weather conditions. In the English countryside blackbirds fed their nestlings mostly on ivy fruit in April and May and cherries (*P. avium* and *P. padus*) in June and July (S n o w & S n o w 1988), and in rocky habitats in Orense (NW Spain) black redstarts fed their offspring on cherries *P. mahaleb* in June and July (G u i t i á n et al. 2001).

The peculiar reproductive cycle of ivy should be pointed out as it is the only European fleshy fruit plant species that flowers at the end of summer and in autumn and starts to ripen at the end of winter and in early spring (S n o w & S n o w 1988, L ó p e z 2001, pers. obs. for the study area). It is therefore of prime ecological importance as a winter and spring source of food for frugivorous birds, lasting only a short period of time (B e r t h o l d 1976b, G u i t i á n 1987, S n o w & S n o w 1988, pers. obs. for the study area). Aggressive intra- and interspecific encounters at ivy plants were probably to defend fruit. It is considered as unusual behaviour and is hardly documented in frugivorous birds (F l e m i n g 1979, S n o w & S n o w 1988, S a l l a b a n k s 1993, pers. obs. for the study area during autumn–winter). Nevertheless, intraspecific attacks could be due in part to paternity guard (B i r k h e a d 1998).

In any case, little is still known about the physiological and ecological significance of fleshy fruit as food for the nestlings and fledglings of partially frugivorous birds, or about the importance of this in different regions and habitats, and further research is needed.

A more specific aspect of feeding fledglings and nestlings worth commenting upon is that in the observed family of blackcaps the female preferred to feed on fruit and the male on arthropods. The reasons for this are not known though intersexual differences in the use of the foraging microhabitat during breeding could be one of them (see W i e n s 1989, H a n o w s k i & N i e m i 1990, for forest passerines). There may also be differences in nutritional requirements, such as the positive selection by females for protein-rich food, like insects, in order to form the eggs in a second or replacement clutch (C l u t t o n - B r o c k 1991), resulting in a greater proportion of fruit being provided to the young. Specialised individual behaviour is also a possibility (see review by B o l n i c k et al. 2003). Male blackbirds visited the ivy plants more frequently than females, which coincides with results obtained by S n o w & S n o w (1988) for England, where 67% of fruit collection between April and June was carried out by males, presumably because during these months the females had to attend to second clutch nests (in this species, nest building and incubation are carried out by the female, C r a m p 1988, present study).

The number of ivy fruits transported each time probably depended on the bill size (blackcap: approximately 7 mm long, C r a m p 1992; blackbird: 17 mm, C r a m p 1988). The blackcaps, though potentially multi-loaders, only transported one fruit at a time. The blackbirds, with a noticeably larger and longer bill, consistently transported several fruits at a time, with a maximum of five. In England blackbirds only managed a maximum of four ivy fruits at once (S n o w & S n o w 1988), perhaps due to their larger size there (almost 9 mm wide and just over 7 mm long on average). Ivy fruit can vary in size even on plants in the same locality (present study).

As for seed dispersal, it would be interesting to carry out detailed studies of the role of adult frugivorous birds as indirect vectors whilst carrying the faecal sacs of nestlings away

from the nest (e.g. dispersal distance, suitability of the places where they leave the sacs). The observed pair of blackcaps placed the faecal sacs on the branches of trees and shrubs, which is quite common behaviour in passerines (O'CONNOR 1985, HERNÁNDEZ 1993), but an unknown percentage of the seeds probably fell to the ground due to rain or other causes. Most of these seeds were intact, that is, their potential germination viability was high. Some faecal sacs of nestlings of frugivorous birds remain in the nests, as was verified in blackbirds, and perhaps a lot of the seeds in them are consumed by rodents. In the study area and other neighbouring ones wood mice use most of the passerine old nests built on shrubs as eating-places and for storing fruit and seeds (HERNÁNDEZ 1994).

Acknowledgements

José María Salgado identified the remains of invertebrates found in the faecal sacs and Andrés Martínez de Azagra and José Requena translated the German bibliography. Comments by an anonymous reviewer improved an earlier draft of the manuscript. I thank Professor C.F. Mason for linguistic revision.

LITERATURE

- BERTHOLD P. 1976a: Über den Einfluß der Nestlingsnahrung auf die Jugendentwicklung, insbesondere auf das Flügelwachstum, bei der Mönchsgrasmücke (*Sylvia atricapilla*). *Die Vogelwarte* 28: 257–263.
- BERTHOLD P. 1976b: Animalische und vegetabilische Ernährung omnivorer Singvogelarten: Nahrungsbevorzugung, Jahresperiodik der Nahrungswahl, physiologische und ökologische Bedeutung. *J. Ornithol.* 117: 145–209.
- BERTHOLD P. 1977: Über die künstliche Aufzucht nestjunger Amseln (*Turdus merula*) mit Beeren des Efeus (*Hedera helix*). *Die Vogelwarte* 29: 110–113.
- BERTHOLD P. 1984: Beeren des Efeus (*Hedera helix*) als Nestlingsnahrung der Mönchsgrasmücke (*Sylvia atricapilla*). *Die Vogelwarte* 32: 303–304.
- BIRKHEAD T. R. 1998: Sperm competition in birds: mechanisms and function. In: Birkhead T. R. & Møller A. P. (eds), Sperm competition and sexual selection. *Academic Press, San Diego*: 579–622.
- BODDY M. 1991: Some aspects of frugivory by bird populations using coastal dune scrub in Lincolnshire. *Bird Study* 38: 188–199.
- BOLNICK D. I., SVANBÄCK R., FORDYCE J. A., YANG L. H., DAVIS J. M., HULSEY C. D. & FORISTER M. L. 2003: The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* 161: 1–28.
- BOSQUE C. & de PARRA O. 1992: Digestive efficiency and rate of food passage in Oilbird nestlings. *Condor* 94: 557–571.
- BREITWISH R., MERRITT P. G. & WHITESIDES G. H. 1984: Why do Northern Mockingbirds feed fruit to their nestlings? *Condor* 86: 281–287.
- CLUTTON-BROCK T. H. 1991: The evolution of parental care. *Princeton University Press, Princeton*.
- CRAMP S. (ed.) 1988: The birds of the western Palearctic, vol. 5. *Oxford University Press, Oxford*.
- CRAMP S. (ed.) 1992: The birds of the western Palearctic, vol. 6. *Oxford University Press, Oxford*.
- FEARE C. 1984: The Starling. *Oxford University Press, Oxford*.
- FLEMING T. H. 1979: Do tropical frugivores compete for food? *American Zoologist* 19: 1157–1172.
- FOSTER M. S. 1978: Total frugivory in tropical passerines: a reappraisal. *Trop. Ecol.* 19: 131–154.
- FOWLER J., COHEN L. & JARVIS P. 1998: Practical statistics for field biology. Second edition. *Wiley, Chichester*.
- GUITIÁN J. 1987: *Hedera helix* y los pájaros dispersantes de sus semillas: tiempo de estancia en la planta y eficiencia de movilización. *Ardeola* 34: 25–35.
- GUITIÁN J., FUENTES M., BERMEJO T., GUITIÁN P., LARRINAGA, A. R. & AMEZQUITA P. 2001: Interactions between the Black Redstart (*Phoenicurus ochruros*) and St. Lucie cherry (*Prunus mahaleb*) in rocky habitats. *Rev. Écol. (Terre Vie)* 56: 81–91.

- GLUTZ von BLOTZHEIM U. 1973: Hartriegelbeeren als Aufzuchtfutter des Grauschnäppers. *Der Ornithol. Beob.* 70: 183–184.
- HAMPE A. 2001: The role of fruit diet within a temperate breeding bird community in southern Spain. *Bird Study* 48: 116–123.
- HANOWSKI J. M. & NIEMI G. J. 1990: Effects of unknown sex in analyses of foraging behavior. *Studies in Avian Biology* 13: 280–283.
- HERNÁNDEZ A. 1993: Dieta de los pollos de tres especies simpátricas de alcaudones (*Lanius* spp.): variaciones con la edad, estacionales e interespecíficas. *Doñana Acta Vertebrata* 20: 145–163.
- HERNÁNDEZ, A. 1994: Micromamíferos utilizando nidos abandonados de aves como almacenes de alimento y lugares-comedor. *Doñana Acta Vertebrata* 21: 186–193.
- HERNÁNDEZ A. 2000: Comensalismo entre pinzones vulgares *Fringilla coelebs* y estorninos negros *Sturnus unicolor* en el consumo de moras *Morus nigra*. *Ardeola* 47: 89–92.
- HERNÁNDEZ A. & ALEGRE J. 1991: Estructura de la comunidad de paseriformes en setos de la provincia de León (NO de España). *Doñana Acta Vertebrata* 18: 237–250.
- HERRERA C. M. 1987: Vertebrate-dispersed plants of the Iberian Peninsula: a study of fruit characteristics. *Ecological Monographs* 57: 305–331.
- HERRERA C. M. 2002: Seed dispersal by vertebrates. In: Herrera C. M. & Pellmyr O. (eds), Plant-animal interactions. An evolutionary approach. *Blackwell Science, Oxford*: 185–208.
- LÓPEZ G. 2001: Los árboles y arbustos de la Península Ibérica e Islas Baleares. *Mundi-Prensa, Madrid*.
- MORTON E. S. 1973: On the evolutionary advantages and disadvantages of fruit eating in tropical birds. *Am. Nat.* 107: 8–22.
- O'CONNOR R. J. 1985: Parental care. In: Campbell B. & Lack E. (eds), A dictionary of birds. *Poyser, Calton*: 432–437.
- RICKLEFS R. E., STARCK J. M. & KONARZEWSKI M. 1998: Internal constraints on growth in birds. In: Starck J. M. & Ricklefs R. E. (eds), Avian growth and development: evolution within the altricial-precocial spectrum. *Oxford University Press, Oxford*: 266–287.
- SALLABANKS R. 1993: Fruit defenders vs. fruit thieves: winter foraging behavior in American Robins. *Journal of Field Ornithology* 64: 42–48.
- SNOW B. K. & SNOW D. W. 1988: Birds and berries. *Poyser, Calton*.
- VEGA-RIVERA J. H., RAPPOLE J. H., MCSHEA W.J. & HAAS C. A. 1998: Wood thrush postfledging movements and habitat use in northern Virginia. *Condor* 100: 69–78.
- WIENS J. A. 1989: The ecology of bird communities. *Cambridge University Press, Cambridge*.