Fruit-feeding behaviour of the European blackbird (*Turdus merula*) on Atlantic ivy (*Hedera hibernica*): variation between the sexes and among locations

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Abstract. I studied the fruit-feeding behaviour of the European blackbird (*Turdus merula*) on plants of Atlantic ivy (*Hedera hibernica* (Kirchner) Bean) at two nearby sites in Galicia in northwest Spain. Feeding behaviour was monitored for a total of 80 hours between December 1997 and March 1998. A total of more than 500 visits and more than 5000 fruit ingestion attempts were observed. Each ingestion attempt was classified as regards mode of access to the fruit (normal, reach-up, reach-down or in-flight) and the fate of the fruit (swallowed, dropped, not-picked or carried-away). For each visit monitored from arrival to departure, I recorded total number of fruits ingested. I also recorded total number of visits per hour, and number of defecations and of regurgitations per hour. Additionally, I characterized each ivy plant as regards inflorescence and fruit characteristics. Most of the plant characteristics determined differed significantly between the two sites: notably, fruit density was much higher at one of the sites. The frequency distribution of mode of access to fruits differed significantly between the two sites but not between the sexes, the between-site difference being due to a difference in the frequency of *reach-down* attempts. Similarly, the frequency distribution of fruit fate differed significantly between the sites but not between the sexes, the between-site difference being due to differences in the frequency of the *dropped* and *carried-away* outcomes. These differences, though statistically significant, were minor in quantitative terms, and in general my findings indicate that feeding behaviour was basically similar at the two sites. Feeding behaviour may have changed over the study period, particularly at the site with higher fruit density, at which fruit density declined dramatically over the study period as a result of blackbird feeding. Finally, most fruits were successfully ingested and few dropped on site, indicating that the European blackbird is an efficient disperser of Atlantic ivy seeds, at least as regards this stage in the dispersal process.
Key words: dispersal efficiency, fruits, feeding behaviour, *Hedera, Turdus.*

Resumen. *Comportamiento de alimentación del mirlo común* (Turdus merula) *sobre frutos de hiedra atlántica* (Hedera hibernica): *variación entre sexos y localidades*. El comportamiento de alimentación se observó durante un total de 80 horas entre diciembre de 1997 y marzo de 1998 en dos localidades del NO de España. Se observaron más de 500 visitas de alimentación y más de 5000 intentos de consumir frutos. Cada intento de consumir un fruto se clasificó en función del modo de acceso al fruto (normal, hacia arriba, hacia abajo, en vuelo) y el destino del mismo (engullido, caído, no arrancado y llevado). En cada visita observada desde la llegada a la salida del ave de la planta, se anotó el número total de frutos consumidos, el número total de visitas por hora y el número de defecaciones y regurgitaciones producidas en la planta por hora. Se caracterizaron las plantas de hiedra en función de las características de la inflorescencia y de los frutos. La mayoría de las características de la planta diferían significativamente entre localidades: especialmente la densidad de frutos fue mucho mayor en una de ellas. La distribución de frecuencias del modo de acceso a los frutos difirió significativamente entre localidades, pero no entre sexos, siendo debida la diferencia entre sitios a las diferencias en el modo *hacia abajo*. De forma similar, la distribución de frecuencias del destino de los frutos fue significativamente distinta entre localidades pero no entre sexos, en este caso la diferencia está en las frecuencias de los destinos *caído* y *llevado*. Estas diferencias, a pesar de ser estadísticamente significativas, fueron pequeñas en términos cuantitativos, y en general, mis resultados indican que el comportamiento de alimentación fue básicamente similar en ambas localidades. Además, sugieren que el comportamiento de alimentación puede haber cambiado a lo largo del período de estudio, especialmente en la localidad con mayor densidad de frutos, en la que la densidad de frutos disminuyó en gran medida durante el período de estudio como resultado del consumo por parte de los mirlos. Finalmente, la mayoría de los frutos fueron consumidos con éxito, y pocos caían a los pies de la planta, lo que indica que el mirlo común es un agente dispersante de alta efectividad para las semillas de la hiedra atlántica, al menos en lo que se refiere a esta fase del proceso dispersivo.

Introduction

Fruit-eating birds and fleshy-fruit-producing plants represent a mutually beneficial relationship, in which the bird receives food and the plant increases the likelihood that its seeds will be dispersed to distant sites (for reviews see Howe & Smallwood, 1982; Janzen, 1983; Dirzo & Domínguez, 1986; Estrada & Fleming, 1986; Stiles, 1989; Jordano, 1992; Fleming & Estrada, 1993).

The capacity of a given disperser species D to transport the seeds of a given plant species P, intact and to an appropriate place for germination and subsequent development, can be considered as the "qualitative" component of D's dispersal effectiveness with regard to P (*sensu* Schupp, 1993). The "quantitative" component is defined as the proportion of seeds of P mobilized by D, with respect to the total number of seeds of P mobilized. Overall dispersal efficiency is the product of the qualitative and quantitative components. Both components can be broken down into numerous individual processes with different effects on the final outcome (Geritz et al., 1984; Bustamante & Canals, 1995). One such process is the transport of seeds from the parent plant to the germination site.

In the present study I investigated 1) the behaviour of the European blackbird (*Turdus merula* L.) while consuming fruits of Atlantic ivy (*Hedera hibernica* (Kirchner) Bean) in two locations in northwest Spain, 2) possible between-sex differences in behaviour, and 3) possible effects of differences between the two locations (notably in fruit abundance) on behaviour. Finally, I consider the consequences of the results obtained for dispersal of *H. hibernica* in the study locations.

Natural history of the plant

Recent studies (McAllister & Rutherford, 1990; McAllister, 1994) have indicated that Atlantic ivy is a separate species from *Hedera helix* L., in view of its ploidy level and morphological characters (trichome type, colour of the leaf veins, etc.). This species, *H. hibernica*, is present in the atlantic coast of the Iberian Peninsula and France. It is a climbing or trailing plant with woody stems and numerous adventitious roots on juvenile branches, which serve to anchor the plant to its support. At my study sites it is the only plant whose fruits are available throughout the winter. It is monoecious, with flowers grouped in umbel-type inflorescences. Both fruits and flowers are morphologically indistinguishable from those of *H. helix*. Some inflorescences have apical umbels only, while others additionally have lateral umbels, the flowers of which open later (Puech, 1989).

The disperser

The European blackbird occurs in a wide range of habitats. Its diet largely comprises earthworms and insects, but fleshy fruits are also important (Guitián, 1984, 1987; Cramp, 1988; Snow & Snow, 1988; Thèry, 1989; Larrinaga, 1998). It is resident in the study area, and Guitián (1987) has reported the following biometric data for individuals captured in the study region in January and February: weight 87.6 g, bill length 24.3 mm, bill width 7.1 mm (n= 37). It shows sexual dimorphism, though the only major biometric difference between the two sexes is in wing length, which is typically slightly greater in males (Cramp, 1988).

Study area

Both study sites (Santiago and Sergude) are located near to the city of Santiago de Compostela in Galicia (northwest Spain), which has a EuropeanAtlantic climate (Carballeira et al., 1983) with rainfall throughout much of the year. The Santiago site is located close to Santiago de Compostela (42°49' N, 8°32' W) in a rural area with a habitat mosaic of cultivated fields, pasture, small patches of seminatural deciduous woodland and larger areas of *Pinus* and *Eucalyptus* plantation; mean temperature throughout the study period (October 1997 - March 1998) was 12.4°C, and rainfall (110 rainy days) was 1486 l/m^2. The Sergude site (42°49' N, 8°27' W) is similar to the Santiago site, with a habitat mosaic of cultivated fields and patches of seminatural deciduous woodland; mean temperature throughout the study period was 12.1°C, and rainfall (103 rainy days) was 1064 l/m^2.

Methods

At both sites, all studies were performed on a single ivy-covered wall (total area 77 m^2 at the Santiago site, 184 m^2 at the Sergude site). In both cases, the ivy on the wall was probably a single individual, though this is difficult to confirm. Umbel density was estimated by counting in four areas of 3 m^2 (Santiago) or eight areas of 2 m^2 (Sergude). The number of fruits per umbel was estimated from 60 randomly selected umbels at each site; these umbels were tagged for subsequent monitoring of phenology and fruit consumption. An additional 120 fruits were randomly selected at each site for characterization of fruit characteristics.

To investigate blackbird feeding behaviour, I made direct observations over a total of 80 h (40 h at each site, between dawn and five hours later, in no case in heavy rain or windy conditions) between January and March 1998, with the aid of 8 x 30 binoculars and a 10 - 50 x 70 telescope. I registered 560 blackbird feeding visits, involving manipulation of more than 5000 fruits. At each visit, I noted the bird's sex, and at each ingestion attempt I noted mode of access to the fruit ("normal", i.e. from the perched position; "reach-up", i.e. reaching upwards with the neck or whole body; "reach-down", i.e. reaching downwards with the neck or whole body; and "in-flight"), and fate of the fruit ("swallowed", "dropped", "not-plucked" or "carried-away"). I also noted the number of fruits eaten during each complete visit (where "complete visit" is defined as a visit fully observed from arrival of the bird at the bush to departure), the number of defecations and regurgitations per hour, and the number of visits per hour.

Mean values of plant and fruit characteristics were compared by Student's *t* tests. The behaviour data showed marked deviation from normality, and were analysed by nonparametric methods (χ^2 goodness-of-fit test, Mann-

Whitney U test, Spearman rank correlation).

Results

Fruit characteristics and production

The principal characteristics of *H. hibernica* plants and fruits at each site are summarized in Table 1. The Santiago plant produced only terminal umbels, while the Sergude plant produced both terminal umbels (until early January) and lateral umbels (from early January onwards), with no overlap in fruiting phenology (Fig. 1).At the Santiago site, umbel density was much higher than at the Sergude site during the period when only terminal umbels were open; however, this difference was less pronounced and not statistically significant after opening of lateral umbels at the Sergude site. Furthermore, mean number of fruits per umbel was greater at Santiago than at Sergude, so that the spatial density of fruits was much higher on the Santiago wall (Fig. 1). As a result, and despite its smaller surface area, the ivy on the Santiago wall bore a greater total number of fruits.

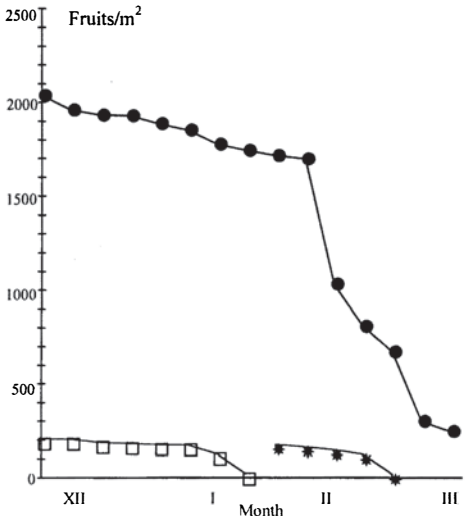


Figure 1. Timecourse of fruit density (fruits/m^2) at the two sites over the study period. Santiago (all terminal umbels): circles. Sergude (terminal umbels): squares. Sergude (lateral umbels): asterisks.

All fruit characteristics considered, except mean individual-fruit fresh weight, differed significantly between the two sites (Table 1). Specifically, fruits were on average shorter but heavier on the Santiago wall than on the Sergude wall. Additionally, mean number of seeds per fruit and mean weight of seeds per fruit were both significantly higher on the Santiago wall, and the mean ratio of pulp weight to seed weight was markedly and significantly lower (Table 1). Terminal-umbel and lateral-umbel fruits from the Sergude wall differed significantly only as regards diameter and fresh weight.

Mode of access to fruits

Considering the pooled data for the two sites (Fig. 2A), the frequency distribution of mode of access to fruits did not differ significantly between male and female birds (χ^2 = 3.64; d.f.=3; p>0.05). In both sexes the "normal" mode predominated (more than 65% of access attempts; n = 3528 for males, n = 1806 for females).The "reach-down", "reach-up" and "in-flight" modes accounted for about 25%, about 6% and about 2% of attempts respectively.

Since no significant between-sex differences were detected, the data for the two sexes were pooled for between-location comparisons (Fig. 2B). The frequency distribution of mode of access to fruits was similar to that observed for the individual sexes (more than 65% of access attempts "normal", about 25% "reach-down", about 6% "reach-up", and about 2% "in-flight"; n=2349 in Santiago, n=2711 in Sergude). However, the frequency distribution

Table 1. Characteristics of plants and fruits at the two study sites. Values shown are means (standard errors, with sample sizes (number of umbels, quadrats or fruits) in brackets. Within each row, means with the same letter do not differ significantly at the 5% level (Student's t tests).

	Santiago	Sergude	
		Terminal umbels	Lateral umbels
Total area (m^2)	76.6	183.76	
Fruits/umbel	30.9±9.6 (60) a	7.4±5.1 (60) b	3.9±3.2 (60) b
Umbels/ m^2	65.8±8.5 (5) a	29.3±7.9 (8) b	51.3±13.8 (8) a
Fruits/ m^2	2,034±262 (5) a	217±58.4 (8) b	200±53.9 (8) b
Total umbels	5,043±650 (5)	5,391±1,451 (8)	9,426±2,540 (8)
Total fruits	155,825±20,065 (5)	38,900±10,733 (8)	36,793±9,906 (8)
Diameter (mm.)	7±0.68 (120) a	6.3±0.66 (30) b	5.85±0.62 (120) c
Length (mm.)	5.76 ±0.38 (120) a	6.26±0.49 (30) b	6.26±0.49 (120) b
Fresh weight (mg.)	147±34 (120) a	134±37 (30) a	121±25 (120) b
Seeds/fruit	3.39±0.80 (120) a	1.57±0.82 (30) b	1.50±0.70 (120) b
Pulp/seed ratio	0.65±0.22 (120) a	1.28±0.44 (30) b	1.15±0.39 (120) b

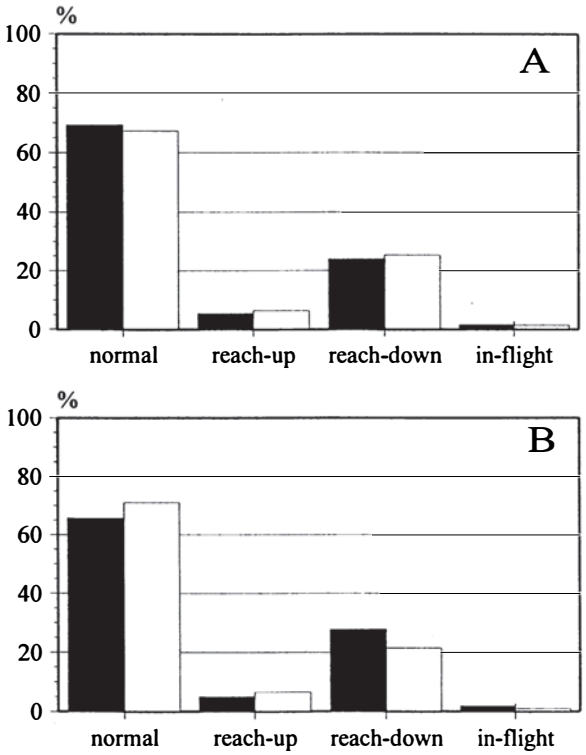


Figure 2. Relative frequencies of the different modes of acces to fruits. A: Comparison of the sexes (black = males; white = females). B: Comparison of the locations (black = Santiago; white = Sergude)

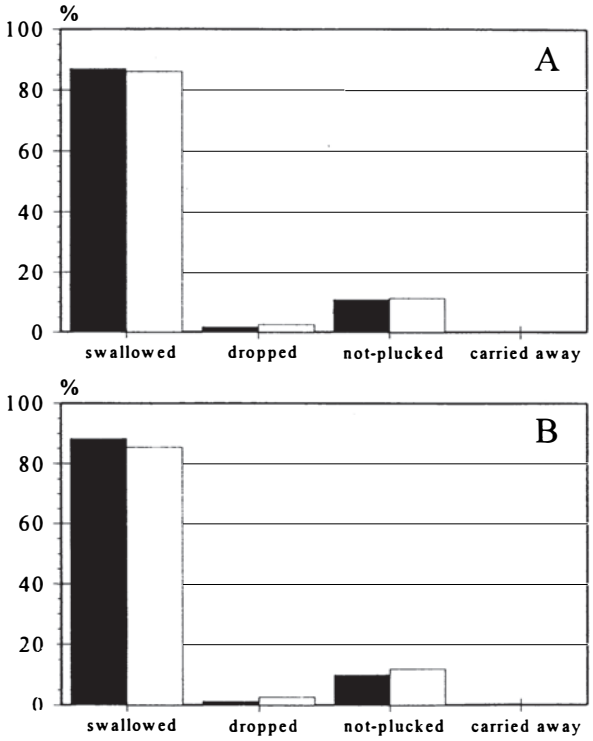


Figure 3. Relative frequencies of the different fruit fates. A: Comparison of the sexes (black = males; white = females). B: Comparison of the locations (black = Santiago; white = Sergude).

differed between the two sites (χ^2=37.73; d.f.=3; p<0.001), which is attributable to the higher proportion of fruits accessed by the "reach-down" mode at the Santiago wall (the contribution of the "reach-down" mode to the overall χ^2 value was +10.9 for the Santiago data, versus -9.61 for the Sergude data).

Fruit fate

Considering the pooled data for the two sites (Fig. 3A), the frequency distribution of fate of fruits did not differ significantly between male and female birds (χ^2=3.65; d.f.=3; p>0.05). Both sexes successfully ingested the majority of fruits manipulated (more than 85%; n=3376 for males, n=2089 for females), while the proportion not-plucked was low (about 11%), and the proportion dropped on site or carried away was very low (< 3% in total).

Considering the pooled data for the two sexes (Fig. 3B), the frequency distribution of fates of fruits differed significantly between the two sites (χ^2=27.03; d.f.=3; p<0.001). This is attributable a) to the higher proportion of "dropped" fruits at the Sergude site (contribution to the overall χ^2 value +5.76, versus -7.29 for the Santiago data), and b) to the higher proportion of "carried away" fruits at the Santiago site (contribution to the overall χ^2 value +4.41, versus -3.61 for the Sergude data). Despite these statistically significant differences, however, the distribution of fates of fruits at the two sites was basically similar: most fruits (more than 80%; n=2659 in Santiago, n=3166 in Sergude) were successfully ingested, a small proportion (<15%) were not picked, and only a very small proportion were dropped or carried away (<5% in both cases).

Other variables

My estimates of number of visits per hour, number of regurgitations per hour, number of defecations per hour and number of fruits ingested per complete visit are listed in Table 2. No significant between-mean differences were detected for any of these variables, either between sexes or between sites (Mann-Whitney U test; n>5; p>0.05 in all cases).

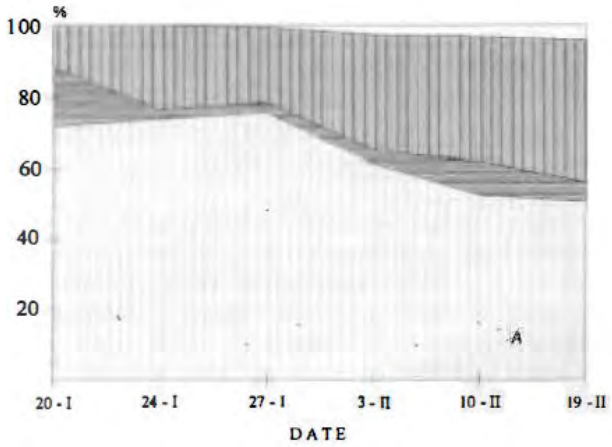
Variation over time

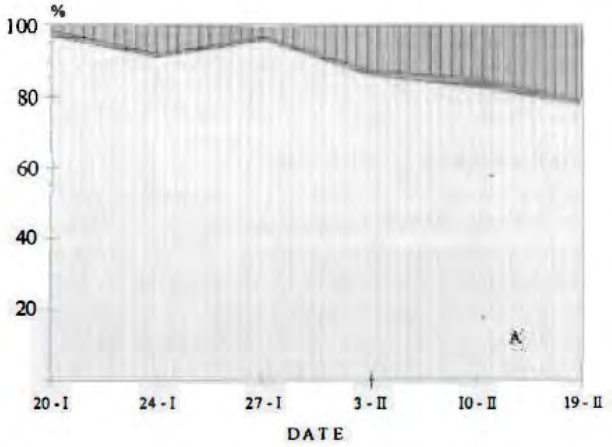
As can be seen from Figure 1, the number of fruits on the plants gradually declined over the study period, very largely as a result of consumption by blackbirds. To investigate whether this had any affect on feeding behaviour, I looked for trends over time in mode of access and fate of fruits.

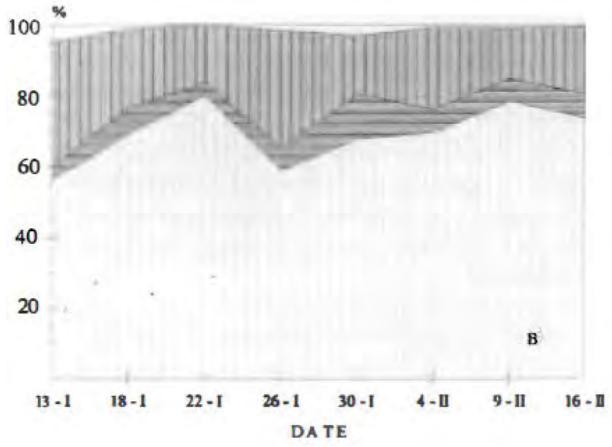
Figure 4 shows the timecourses of the relative frequency distributions of mode of access at the two study sites. Considering the Santiago data, there was a significant negative correlation between fruit density and the relative frequency of the "in-flight" mode (r_s=-0.939, n=6 monitoring days, p<0.01); fruit density was not significantly correlated with any of the other relative frequencies, though the correlation with the relative frequency of the "reach-up" mode was close to significance at the 5% level (r_s=-0.707, n=8, p=0.057). Considering the Sergude data, there were no significant correlations at the 5% level between fruit density and relative frequency of mode of access. Furthermore, the plot of the Sergude data (Fig. 4B) shows no clear trend, by contrast with the plot of the Santiago data (Fig. 4A).

Table 2. Summarized data on feeding behaviour at the two study sites, showing a) number of fruits eaten per complete visit (see text), b) number of visits per hour, c) number of defecations per hour, and d) number of regurgitations per hour. Values shown are mean±SE, with sample size (i.e. number of observation days) in brackets.

	N.° fruits eaten/c.v.		Visits/hour		Defecations/hour		Regurgitations/hour	
	Santiago	Sergude	Santiago	Sergude	Santiago	Sergude	Santiago	Sergude
Male	12.31±7.06	15.34±5.03	6.61±5.37	4.94±2.75	0.78±0.93	0.29±0.19	0.56±0.75	0.45±0.36
	(16)	(26)	(6)	(8)	(6)	(7)	(6)	(7)
Female	16.66±6.28	12.9±6.82	3.10±2.50	3.71±1.9	0.32±0.56	0.52±0.55	0.60±0.43	0.68±0.40
	(16)	(20)	(6)	(8)	(6)	(7)	(6)	(7)
Total	13.5±6.99	14.35±5.89	9.71±6.98	8.65±2.90	1.1±1.47	0.81±0.48	1.16±0.81	1.13±0.67
	(32)	(46)	(6)	(8)	(6)	(7)	(6)	(7)







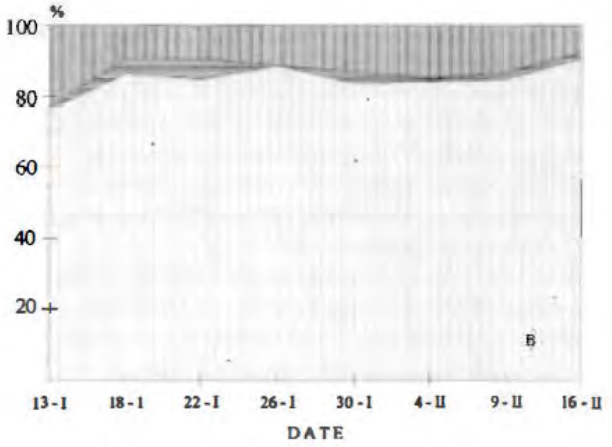


Figure 4. Timecourse of relative frequencies of modes of access to fruit over the study period. A - Santiago, B - Sergude. Dotted area: normal. Horizontal hatching: reach-up. Vertical hatching: reach-down. White: in-flight. Each point shows the relative frequency on a single day of monitoring.

Figure 5. Timecourse of relative frequencies of fruit fates over the study period. A - Santiago, B - Sergude. Dotted area: swallowed. Horizontal hatching: dropped. Vertical hatching: not-picked. White: carried-away. Each point shows the relative frequency on a single day of monitoring.

Equivalent plots of the data on fruit fate are shown in Figure 5, and reveal a similar pattern to that observed for mode of access: the plot of the Santiago data (Fig. 5A) shows a clear trend, unlike the plot of the Sergude data (Fig. 5B). However, relative frequencies of fruit fates were in no case significantly correlated with fruit density ($r_s < 1$, n = 6 for Santiago, n = 8 for Sergude, $p > 0.05$ in both cases).

Dicussion

Plant characteristics

Puech (1989) studied variation in flower, inflorescence and fruit morphology in *H. helix*, and found three characteristic types, which he designated m, l and r, distinguishable by umbel type, number of fruits per umbel and fruit

characteristics (largely fruit size and number of seeds). Each individual presents a single morphological type, which remains constant throughout the lifespan. My findings suggest that this pattern is likewise present in *H. hibernica*, with the Santiago plant being type l (terminal umbels with numerous fruits, fruits of lateral umbels aborted) and the Sergude plant type r (terminal umbels with fewer fruits, fruits of lateral umbels not aborted).

Fruit characteristics are consistent with this assumption. Specifically, there were marked between-site differences in almost all fruit characteristics, particularly pulp-to-seed ratio. Note, however, that Obeso & Herrera (1994) have reported that pulp-to-seed ratio shows great variation within individuals of *H. helix*, but little variation among individuals. In the present study, each site was probably occupied by a single individual (though I cannot be certain of this, since it is difficult to distinguish individuals in the field), so that my results may not be representative at plant species level, and not strictly comparable to Obeso & Herrera (1994) results.

Blackbird feeding behaviour

In general, birds access fruits by the method with lowest energy cost (Moermond et al., 1986). In the case of the European blackbird, these methods appear to be "normal" mode (i.e. from the perch without evident stretching) and "reach-up" mode (i.e. stretching the neck or body upwards). The "reach-down" mode (i.e. stretching the neck or body downwards) and "in-flight" mode were much less frequently used, though they became more frequent on the Santiago wall when fruit density dropped towards the end of the study period, suggesting that they are used when the favoured strategies become unproductive. One possible explanation for the low frequency of the "reach-down" and "in-flight" modes is that they have a higher energy cost.

I did not detect any significant between-sex difference in feeding behaviour, suggesting that the morphological differences existing between the sexes are insufficient to cause differences in feeding behaviour, at least when feeding on *H. hibernica* in this study area.

However, I did detect significant between-location differences, in both feeding behaviour and fruit fate. The feeding behaviour of frugivorous birds may be affected by both plant characteristics (Moermond & Denslow, 1983) and the characteristics of the bird itself, whether morphological (Moermond et al., 1986; Larri-naga, 1997, 1998) or behavioural (Rodríguez & Bermejo, 1995). It is possible that the between-location differences observed were due to pre-existing differences in the behavioural tendencies of the blackbirds feeding at each site, rather than to between-location differences in plant characteristics. This possibility would be difficult to rule out if only a small number of individuals were feeding at each site; however, my observations suggest that at least 10 individuals regularly fed at each site over the study period. It therefore seems more likely that the between-location differences in feeding behaviour reflected differences in plant characteristics. Nevertheless, colour-ringing and subsequent monitoring of individual birds would be necessary to confirm this.

Assuming that the between-location differences in feeding behaviour reflected differences between the plants, the plant characteristics potentially involved are numerous, and might include fruit size, fruit density, between-fruit distance, between-infructescence distance, branch diameter, branch flexibility, etc. In the present context, unequivocal identification of the characteristics that determine feeding behaviour would require detailed studies involving experimental manipulation of the plant. However, some useful information can be gained by statistical analyses of relationships between plant characteristics and the frequency of particular behaviours. Although we detected only one statistically significant correlation (between fruit density and the relative frequency of the "in-flight" mode, on the Santiago wall), the plot of the timecourses of relative frequencies of modes of access for the Santiago wall (Fig. 4A) shows what appears to be a clear trend, which may be related to the sharp decline in fruit density observed over the study period (Fig. 1). On the Sergude wall, by contrast, fruit density remained roughly constant over the study period, which is consistent with the absence of any apparent change in the relative frequencies of mode of access at this site.

Despite the between-location differences in behaviour observed in the present study and in previous studies (Larrinaga, 1998), the European blackbird shows morphological characteristics and behavioural flexibility which ensure fairly consistent success while feeding on fruits. Most ingestion attempts are successful. Most attempts are "normal" mode, with the "reach-down" mode being the second most frequent (see for example Herrera & Jordano, 1981, and Rodríguez & Bermejo, 1995, for similar results with *Prunus mahaleb*; Snow & Snow (1988) for results with various species of plant; Larrinaga (1998) for results with *Crataegus monogyna*; and Guitián (1987) for results with *Hedera helix*). The high success rate of the European blackbird (i.e. most fruits ingested, few dropped) suggests that it is consistently efficient as regards this stage in seed dispersal, though evaluation of overall efficiency would of course require consideration of other factors (e.g. effects on the seed of passage through the digestive tract, site of deposition, etc.).

In conclusion, it seems likely that the observed differences in fruit characteristics between the two sites considered in the present study gave rise to minor differences in the behaviour of the blackbirds feeding at each site. However, these differences in behaviour were probably too small to have any ecologically significant effect on the efficiency of seed dispersal.

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