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Behaviour of redwing (*Turdus iliacus L.*) during feeding on berries of hawthorn (*Crataegus monogyna*)

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ABSTRACT.-*Behaviour of redwing* (Turdus iliacus L.) *during feeding on berries of hawthorn* (Crataegus monogyna). The behaviour of redwings was monitored during feeding on hawthorn berries at several sites in Scotland and northwest Spain. The birds generally visited hawthorn bushes in small monospecific groups. The mean time spent by each bird on each bush was 100 s. The mean number of `berry-ingestion attempts` per minute was 5.5, and about 63% of attempts were successful. During a bird`s feeding bout to a single bush, the berries ingested tended to be close to each other. Posture while feeding was generally similar to resting posture. Mean distance between the berries ingested during a feeding bout varied significantly among the sites, probably reflecting variation in bush structure and fruit availability.

KEY WORDS. Frugivory, feeding behaviour, seed dispersal, *Turdus iliacus*, *Crataegus monogyna*.

Introduction

The pulp of fleshy fruits is an important food resource for frugivorous birds, while seed dispersal by such birds is often important to the plant (Jordano, 1982; Courtney & Manzur, 1985; Snow & Snow, 1988; Fuentes, 1992; Jordano, 1992; Levey, 1993). A number of researchers have investigated aspects of bird behaviour during frugivory (Herrera & Jordano 1981; Guitián, 1989; Greenberg et al., 1993; Shupp, 1993), or have specifically studied food-item selection, generally with birds in captivity (Moermond & Denslow, 1983; Levey et al., 1984; Moermond et al., 1986; Santana et al., 1986; Moermond et al., 1987; McPherson, 1988). However, there have been very few detailed field studies of behaviour while feeding on fleshy fruits (though see Pratt & Stiles, 1983; Santana and Milligan, 1984; Godschalk, 1985; Foster, 1987; Rodríguez & Bermejo, 1995).

The feeding behaviour of frugivorous birds during long-distance north-south migration is of particular interest. Specifically, changes in hours-of-daylight, together with features of long-distance migration such as intensified social interaction and increased energy outlay, may have effects on feeding behaviour and thus on seed dispersal.

The aims of the present study were to describe the behaviour of the redwing (*Turdus iliacus*) during feeding on berries of hawthorn (*Crataegus monogyna*). To investigate possible influences of

latitude and migratory stage, behaviour was monitored during the migratory period at several sites in Scotland, Wales and northwest Spain.

Species Studied

Redwing (*Turdus iliacus* L.)

The redwing is a migratory species with a body weight of about 70 g. Its breeding range covers northern Europe, from Iceland through Scandinavia and Poland to eastern Siberia; during the present century it has begun to breed in Scotland and parts of England. It winters in Central and Western Europe, including Great Britain and the Iberian Peninsula, as well as the southern Baltic region and the Balkans, and also around the Aral Sea, on the southern shores of the Caspian, and in coastal areas of Asia Minor, the Lebanon and the Maghreb, occasionally reaching as far as the Nile delta (Cramp, 1988).

The redwing's diet comprises a wide range of invertebrates (Debussche & Isenmann, 1985; Cramp, 1988) plus fleshy fruits in the autumn and winter (Guitián, 1984; Courtney & Manzur, 1985; Debussche & Isenmann, 1985; Cramp, 1988; Snow & Snow, 1988; Soler et al., 1988; Fuentes, 1992; Guitián, 1989; Guitián & Fuentes, 1992).

Hawthorn (*Crataegus monogyna* Jacq.)

The hawthorn is a woody Rosacea which is common in thornscrub in northwest Iberia (Guitián et al., 1992), in which it may account for up to 56% of woody species cover (Fuentes, 1992). In Great Britain, on the other hand, hawthorn generally occurs in hedgerows, though it may occasionally occur in scrub or woodland (Courtney & Manzur, 1985).

In the northwest Iberian Peninsula, flowering starts at the end of April and lasts for about a month (Guitián et al., 1992). The fruit develops throughout the summer, with ripe fruit density peaking between mid-September and mid-October, depending on year (Fuentes, 1992; Guitián & Fuentes, 1992). The period of fruit availability is long, continuing until as late as early February. Throughout this period the blackbird (*Turdus merula* L.) is the principal consumer of fruits, followed by other thrush species (song thrush *T. philomelos* Brehm, mistle thrush *T. viscivorus* L., fieldfare *T. pilaris* L., and redwing *T. iliacus* L.); this is generally the case both in Great Britain (Courtney & Manzur, 1985; Snow & Snow, 1988) and in the northwest Iberian Peninsula (Fuentes, 1992; Guitián & Fuentes, 1992). However, redwing or fieldfare may be the principal consumers for short periods when large migratory bands pass through on passage, and indeed in the northwest Iberian Peninsula redwings may in some years be the principal consumers of hawthorn berries throughout the winter (personal observation).

Study Area

The study was carried out at four sites along a latitudinal gradient running through Great Britain and the northwest Iberian Peninsula. At all four sites considerable passage of redwings was observed between early October and mid-November.

The two most northerly sites (Golspie, 57o55'N, altitude < 50 m asl, and Taynuilt, 56o25'N, altitude likewise < 50 m asl) are in coastal locations in Scotland, and have very similar climate, vegetation and relief. At both sites hawthorn is the dominant component of hedgerows which act as boundaries between fields dedicated to grazing.

The third site is at Dolgellau in north Wales (52o44'N, altitude about 100 m asl). Although this site is at higher altitude and is located a few kilometres from the coast, it has an oceanic climate similar to - though somewhat warmer than - that of the Scottish sites. Hawthorn is present as single individuals scattered over boggy grazing land, where it is the dominant woody species. Mountain ash (*Sorbus aucuparia*), blackthorn (*Prunus spinosa*), holly (*Ilex aquifolium*) and oak (*Quercus robur*) are also present.

The fourth site is at La Barosa (42o30'N, altitude 450 m asl), in the El Bierzo region of north-

west Spain. This site has clearly Mediterranean characteristics, and is different from the rest in that hawthorn there forms part of a woodland fringe community with very high woody-species cover (92.5%, about 56% of which is due to hawthorn, the dominant species; Fuentes, 1992). This community represents a degradation state of the natural holm oak woodland which is dominant in this area.

Methods

Feeding behaviour was monitored by direct observation with binoculars (10 x 50) and a telescope (Celestron 1000 mm, with 26 and 33 mm eyepieces) during October, November and December 1991 and 1992. Total observation time was 5.5 h in Golspie, 20.5 h in Taynuilt, 16 h in Dolgellau and 21.5 h in La Barosa. A total of 294 feeding feeding bouts and 1,435 berry-ingestion attempts were recorded.

Ten variables were determined, four (a - d) relating to individual berry-ingestion attempts and six (e - j) to feeding bouts:

a) Between-berry distance;
b) Bird-to-berry distance;
c) Attempt method;
d) Attempt outcome;
e) Feeding bout duration;
f) Number of berry-feeding attempts during feeding bout;
g) Distance to each of nearest five birds;
h) Species of each of nearest five birds;
i) Attempt rate;
j) Fruit mobilization efficiency.

Between-berry distance was the distance between the berry being attempted and that previously attempted, estimated on a six-point scale (0 - 5 cm, 5 - 10 cm, 10 - 15 cm, 15 - 20 cm, 20 - 25 cm, > 25 cm) by visual reference to the length of the bird (taken to be 21 cm). Bird-to-berry distance was the distance between the berry being attempted and the feet of the bird, estimated on a seven-point scale (0 - 5 cm, 5 - 10 cm, 10 - 20 cm, 20 - 30 cm, 30 - 40 cm, 40 - 50 cm, > 50 cm), again by reference to the length of the bird. Attempt method was classed as "pick" (berry-ingestion attempt from a posture similar to resting posture, without apparent effort), "reach up" or "reach down" (evident difficulty in reaching the berry), or "snatch" (in flight) (see Moermond et al., 1986). Attempt outcome was classed as "swallowed", "dropped", "carried away", "pecked" (i.e. some flesh eaten without removing berry) or "unplucked" (i.e. berry neither removed from bush nor pecked).

A bird's feeding bout to a bush was defined as the period during which the bird was observed on the bush; note, however, that this period was often shorter than the real feeding bout. Attempt rate is a derived variable, calculated as [number of attempts during feeding bout] / [feeding bout duration (min)]. Fruit mobilization efficiency is likewise a derived variable, calculated on the basis of numbers of each attempt outcome as [swallowed + carried-away] / [swallowed + carried-away + dropped]; unplucked and pecked berries were excluded from the calculation since the eventual fate of such berries is not known. Note that fruit mobilization efficiency is only one of the major components of seed dispersal efficiency (see Discussion).

Unless otherwise stated, statistical significance is taken to be indicated by p values of less than 0.05.

Results

Pooled data (all sites)

Between-berry distance was typically short (mode 0 - 5 cm, median 0 - 5 cm, range 0 - 150 cm), and was nonuniformly distributed over the range considered (Kolmogorov-Smirnov goodness-of-fit test, $Z = 10.59$, $p < 0.001$, fig. 1). Bird-to-berry distance was likewise nonuniformly distributed over the range considered (Kolmogorov-Smirnov goodness-of-fit test, $Z = 10.72$, $p < 0.001$), with shorter distances being more frequently observed (mode 5 10 cm, median 5 - 10 cm, range 2 - 30 cm, fig. 2).

The most frequent attempt method was "pick" (64.1% of attempts), followed by "reach down"

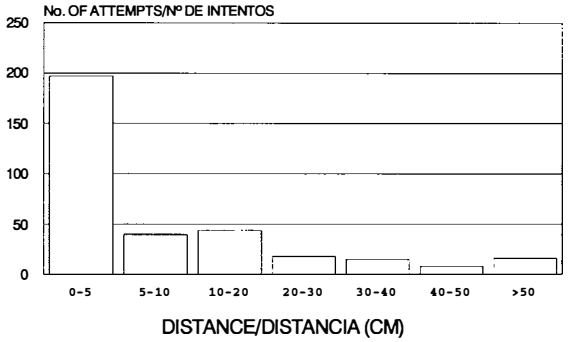

Figure 1. Frequency distribution of between-berry distance for all consecutive pairs of berry-ingestion attempts.
[Distribución de frecuencias de las distancias entre dos frutos manipulados consecutivamente por el ave.]

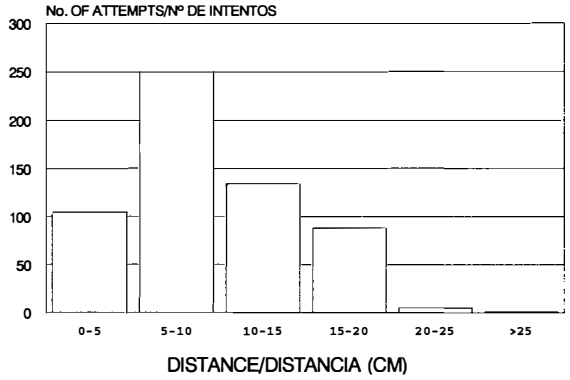

Figure 2. Frequency distribution of bird-to-berry distance for all berry-ingestion attempts.
[Distribución de frecuencias de las distancias de las patas del ave al fruto que intenta consumir.]

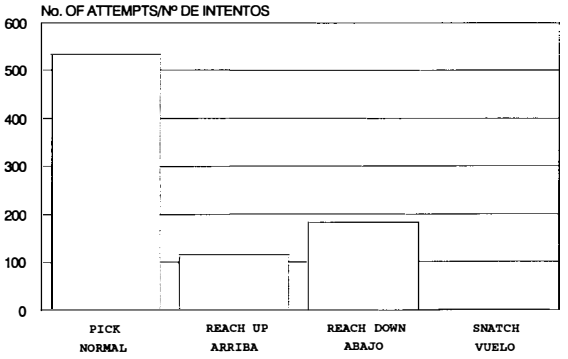

Figure 3. Frequency distribution of method for all berry-ingestion attempts.
[Frecuencias de utilización de los distintos modos de acceso al fruto.]

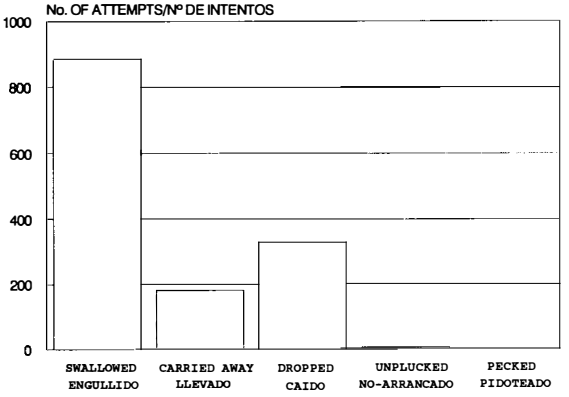

Figure 4. Frequency distribution of outcome for all berry-ingestion attempts.
[Frecuencias de los destinos de los frutos manipulados.]

(22.0%) and "reach up" (13.8%) (fig. 3). Berries were almost never taken in flight (< 0.1%), and redwings were never seen to feed on berries on the ground.

The most frequent attempt outcome was "swallowed" (63% of attempts), followed by "unplucked" (22%) and "dropped" (13%) (fig. 4). Very few berries were "carried away" (0.6%) or "pecked" (< 0.1%).

Considering complete feeding bouts only (i.e. feeding bouts monitored from arrival to departure), feeding bout duration ranged from 19 to 439 s (n = 22; mean = 100 s; s.d. = 131 s). Again considering complete feeding bouts only, number of attempts during feeding bout ranged from 1 to 15 (n = 19; mean = 5.5; median = 5). Considering all feeding bouts (complete and incomplete), mean attempt rate was 5.4 attempts per minute (s.d. = 3.78), and mean fruit mobilization efficiency was 0.84 (s.d. 0.25).

Distance to each of nearest five birds ranged from 10 cm to 3 m (mean 74 cm, median 60 cm, mode 60 cm). The nearest neighbours were most frequently

Table I. Spearman`s coefficients of correlation between mean distance to the five nearest neighbours and a) mean between-berry distance for all consecutive pairs of berry-ingestion attempts, b) mean bird-to-berry distance for all berry-ingestion attempts, c) fruit mobilization efficiency, d) mean number of berry-ingestion attempts per minute, e) feeding bout duration (sec), and f) number of berry-ingestion attempts during a feeding bout.
[Coeficiente de correlacion de Spearman de la distancia media a los pájaros más cercanos con a) distancia media entre frutos consecutivos, b) distancia media del ave a los frutos que intenta consumir, c) eficiencia de movilización, d) tasa de intentos, e) duración de la visita en segundos, f) número de intentos por visita.]

	A	B	C	D	E	F
r_s	0,1266	0,0049	-0,0198	-0,1691	0,4750	0,4186
(n)	(94)	(145)	(164)	(143)	(19)	(22)
p	0,224	0,954	0,802	0,043	0,040	0,053

redwings (92.5% of feeding bouts), followed by blackbirds (3.1%), fieldfares (1.3%) and robins (Erithacus rubecula) (0.6%). Distance to nearest five birds (mean for each feeding bout) showed a significant positive correlation with feeding bout duration, a near-significant (p = 0.053) positive correlation with number of attempts during feeding bout, and a weak but significant negative correlation with attempt rate (table I).

No relationship was detected between attempt method and attempt outcome (c2 = 7.30, d.f. = 4. p > 0.05; category "carried-away", with a single fruit, excluded from the analysis). Similarly, there was no significant relationship between attempt outcome and bird-to-berry distance (Kruskall-Wallis test, H = 5.40, p > 0.05). These findings suggest that berries which are further from the bird, and apparently more difficult to reach, are no more likely to be dropped than nearby berries.

Mean bird-to-berry distance during each feeding bout was not significantly correlated with fruit mobilization efficiency (Spearman's r (rS) = 0.01, n = 138, p > 0.05).

Mean between-berry distance during each feeding bout showed a significant negative correlation with attempt rate (rS = -0.22, n = 78, p < 0.05).

Table II. Cross-classified data on berry-ingestion attempt method at the La Barosa, Taynuilt and Golspie sites, showing a) cell frequency, b) deviation (+ or -) with respect to the frequency expected assuming no association, and c) estimated contribution of that cell to the overall chi-squared value (c2 = 22.39, d.f. =4, p< 0.001). The frequency of the attempt method `snatch` was negligible at all sites. Berry-ingestion atttempt method data were not collected at Dolgellau.
[Resultados del análisis de la variación latitudinal de los modos de acceso a los frutos en La Barosa, Taynuilt y Golspie. Se indica en cada caso frecuencia absoluta, signo de la desviación con respecto a las frecuencias esperadas y contribución a la c2 total de cada modo (c2 =22,39, d.f.=4, p<0,001)].

	La Barosa 42°30'N	Taynuilt 56°25'N	Golspie 57°55'N
pick	416	101	17
	+	-	-
normal	0,09	0,25	0,01
reach up	73	40	2
	-	+	-
arriba	2,56	12,96	0,81
reach down	151	24	8
	+	-	+
abajo	0,81	4	0,64

Table III. Cross-classified data on berry-ingestion attempt outcome at the La Barosa, Dolgellau, Taynuilt and Golspie sites, showing a) cell frequency, b) deviation (+, - or 0) with respect to the frequency expected assuming no association, and c) estimated contribution of that cell to the overall chi-squared value ($c2 = 15.81$, d.f.= 4, $p < 0.05$). Mobilized = 'swallowed'+ 'carried away'. Left = 'pecked'+ 'unplucked'. [Resultados del análisis de la variación entre localidades de los destinos de cada fruto, para las localidades de La Barosa, Dolgellau, Taynuilt y Golspie. Se indica en cada caso frecuencia absoluta, signo de la desviación (+, - ó 0) respecto a las frecuencias esperadas y contribución a la c2 global de cada destino ($c2 = 15,81$, d.f.= 4, $p < 0.05$).]

	La Barosa 42°30'	Dolgellau 53°	Taynuilt 56°25'	Golspie 57°55'
mobilized	405	78	401	11
[movilizados]	0	+	0	-
	0	0,64	0	2,56
dropped	72	14	88	9
	-	-	+	+
[caídos]	1,44	0,01	0,49	7,84
unplucked + pecked	160	20	142	8
[no arrancados +	+	-	-	+
picoteados]	0,81	1,44	0,25	0,36

There was no significant correlation between attempt rate and proportion of attempts with outcome "dropped" ($rS = -0.14$, $n = 143$, $p > 0.05$).

Between-site variation

Mean bird-to-berry distance (not recorded at Dolgellau) was lowest at Golspie, intermediate at Taynuilt and highest at La Barosa, and varied significantly among sites (Kruskall-Wallis test, $H = 9.94$, $p < 0.01$). Subsequent multiple comparisons testing (Conover, 1980) indicated significant differences between La Barosa and both Taynuilt and Golspie, but not between Taynuilt and Golspie.

Attempt method showed significant dependence on site ($c2 = 22.39$, d.f. = 4, $p < 0.001$; the category "snatch", containing a single attempt, was excluded from the analysis). The significant c2 is largely due to the high frequency of "reach up" and the low frequency of "reach down" at Taynuilt (table II).

Attempt outcome likewise showed significant dependence on site ($c2 = 15.81$, d.f. = 6, $p < 0.05$). Note, however, that this result is largely due to the observed frequencies at Golspie, where sample size was small (table III).

The remaining variables showed no significant dependence on site (between-berry distance - Kruskall-Wallis test, $H = 1.99$, $p > 0.05$; attempt rate - $H = 0.86$, $p > 0.05$; fruit mobilization efficiency - $H = 4.99$, $p > 0.05$; proportion of berries dropped at each feeding bout - $H = 4.56$, $p > 0.05$; distance to nearest five birds - $H = 0.04$, $p > 0.05$).

Discussion

When feeding on hawthorn, redwings feed largely on berries which are close to them. Consecutive berries are usually close to each other. Proximity and accessibility thus appear to be important determinants of fruit selection. Previous studies of frugivorous birds have suggested that selection on the basis of accessibility may often entirely over-ride other selection criteria (Moermond & Denslow, 1983; Moermond et al., 1986; Santana et al., 1986; Moermond et al., 1987). Behaviour of this type indicates that the feeding strategy is strongly influenced by the need to minimize energy outlay per food item ingested (Moermond et al., 1986; Moermond et al., 1987).

A study by Paszowski (1982) indicated that the American robin (*Turdus migratorius* L.) accesses 88% of fruits in flight when feeding on Amelanchier laevis Wiegand. In the present study, redwings hardly ever accessed hawthorn berries in flight. Amelanchier laevis has very thin branches, and a large turdine like the American robin is thus probably obliged to access the fruits of this species in flight.

The relatively low frequency of "reach up" and "reach down" berry-ingestion attempts is in accordance with field observations of the blackbird (*Turdus merula*), the black redstart (*Phoenicurus ochruros* Gmelin) and the blackcap (*Sylvia atricapilla* L., 1758) (Rodríguez & Bermejo, 1995), and with laboratory studies of tropical frugivorous birds (Moermond & Denslow, 1983; Moermond et al., 1987). Such behaviour may reflect morphological limitations due to pre-adaptation to other types of food (Moermond et al., 1986; Jordano, 1992).

Fruit mobilization efficiency as defined in the present study is of course only a crude and incomplete estimate of the real value of seed dispersal efficiency, which has other important components in addition to efficiency of removal from the site by the bird (see Schupp, 1992). However, fruit mobilization efficiency constitutes a useful basis for between-species comparisons. The values obtained in the present study are considerably lower than those obtained by Rodríguez & Bermejo (1995) for fruits of Prunus mahaleb L. by Turdus merula, Phoenicurus ochruros and Sylvia atricapilla, lower than those obtained by Herrera & Jordano (1981) for fruits of P. mahaleb by Turdus merula and Sylvia atricapilla, and higher than that obtained by Herrera & Jordano (1981) for fruits of P. mahaleb by Phoenicurus ochruros. Note that the latter authors considered "unplucked" fruits to be "not-mobilized".

The data on distance to nearest neighbours, and on the species of nearest neighbours, indicate that redwings typically feed on hawthorn in small loose flocks, as reported previously for this species and for blackbird (Guitián & Fuentes, 1992). Feeding in flocks probably allows each individual to dedicate less time to vigilance and more time to feeding (Caraco et al., 1980; Guitián & Fuentes, 1992); this interpretation is supported by the negative (though admittedly weak) correlation between the rate of berry-ingestion attempts and mean distance from the five nearest neighbours. Aggressive interactions were very scarce.

Behavioural differences related to differences in site latitude or migrational stage might be expected to have effects on variables such as attempt rate, fruit mobilization efficiency, proportion of berries dropped or distance to nearest neighbours; however, none of these variables showed significant variation among sites. Between-site variation was observed in a number of other variables, but in these cases was probably due to between-site differences in hawthorn stand characteristics rather than migrational stage. For example, the higher bird-to-berry distances at La Barosa than at the Scottish sites probably reflects the fact that hawthorn at the latter sites forms dense hedgerows, in which the majority of fruits are readily accessible from a nearby perch; at La Barosa, by contrast, the plants are more widely spaced and have a more open structure, so that there are fewer perching sites. Alternatively, fruit density may have been lower at the Spanish site (because of lower production, or because this site was monitored later in the fruiting season). Fruit density and abundance has previously been reported to have important effects on bird foraging behaviour (see for example Sallabanks, 1992, 1993, for studies of the behaviour of Turdus migratorius on hawthorn).

The larger proportion of berries dropped at Golspie may indicate a higher rejection rate (perhaps because of insect or fungal damage) or manipulation difficulties (because of differences in size, weight or shape, for example). In 1992, fruits were longer, broader and heavier at a site in the Golspie area (16 km from that of the present study) than at

Taynuilt and Dolgellau; in 1994, fruits were longer at the Golspie site than at Taynuilt and Dolgellau, but broader at Dolgellau than at the other two sites (unpublished data). These data suggest a possible effect of latitude, at least on fruit length.

Apart from redwings, the principal disperser of hawthorn seeds in Great Britain appears to be Turdus merula (Hartley, 1954; Snow & Snow, 1988; unpublished data). The proportion of hawthorn berries dropped by Turdus merula does not appear to be any larger at northern sites than at southern sites (unpublished data). This may mean that redwing migration may have a negative effect on the dispersion of hawthorn seeds in more northerly populations.

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Resumen

Los frutos del espino blanco constituyen un importante componente en la dieta del zorzal alirrojo durante la migración otoñal. Durante Octubre, Noviembre y Diciembre de 1991 y 1992 se estudió el comportamiento de alimentación del zorzal alirrojo cuando consume frutos de espino blanco o majuelo en cuatro localidades a lo largo de su ruta de migración (dos en Escocia, una en Gales y una en el noroeste de la Península Ibérica).

Para cada visita de alimentación (de un pájaro a un pie de majuelo) se registraron los siguientes datos: a) duración de la visita, b) número de intentos de consumo de un fruto, c) método de cada intento (normal, arriba, abajo y vuelo, ver Moermond et al., 1986), d) resultado de cada intento (fruto engullido, picoteado, llevado, caído o no arrancado), e) distancia aproximada entre frutos de intentos consecutivos, f) distancia aproximada entre el pájaro en observación y los cinco vecinos más proximos (y especie de cada vecino). Posteriormente se calcularon las siguientes variables: a) número medio de intentos de consumo de fruto por minuto y b) eficacia de movilización por visita ([engullidos+llevados]/ [engullidos+llevados+caídos]).

Los zorzales alirrojos tendían a coger frutos cercanos a ellos (fig. 2), e intentos consecutivos tendían a estar dirigidos hacia frutos cercanos entre sí (fig. 1). Los intentos de consumo se realizaban generalmente desde una postura normal, con poco esfuerzo aparente (fig. 3). La mayoría de los frutos que intentaban consumir eran engullidos con éxito y un 13% de ellos caían (fig. 4). La eficacia media de movilización era 0,84. La duración media de la visita era de 100 s, y el número medio de intentos por minuto era de 5,5. Ninguna de las variables registradas estaba significativamente asociada con la proporción de frutos caídos o con la eficacia de movilización.

La media del promedio de las distancias a los cinco vecinos más cercanos fué de 74 cm y éstos eran generalmente otros zorzales alirrojos.

La distancia media a los cinco vecinos más cercanos por visita estaba correlacionada negativamente con el número de intentos por minuto (tabla I), lo que podría reflejar diferencias en el tiempo dedicado a la vigilancia.

Las distancias medias entre el fruto y los pies del ave variaron entre localidades. Ésto probablemente refleja diferencias en la estructura del árbol (los pies estudiados en Escocia forman parte de setos manejados, mientras que los de la Península Ibérica forman parte de comunidades de orla de bosque) o densidad de frutos. El método de intento también varió significativamente entre localidades (tabla II).

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