# Patterns of migration and wintering of Robins Erithacus rubecula in northern Iberia

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The aim of this study was to analyse the patterns of migration and wintering of European Robins *Erithacus rubecula* in northern Iberia (Plaiaundi Ecological Park, Irún, N Spain). Overall, 185 Robins were ringed at weekly trapping sessions from September 2004 to April 2005. The temporal distribution of abundance and recaptures indicated that the autumn migration period lasted from September to November, the winter period from November to February, and the spring migration from March to April. Some wintering Robins arrived earlier than most of the migrants which passed through the area in autumn, whilst most left the area before the majority of spring migrants appeared. First-winter Robins were always more abundant than older birds, and females more abundant than males. Morphological traits varied only in relation to sex, and it was not possible to distinguish between migrating and wintering Robins from measurements. Overall, body mass and fuel load were low during both the autumn and spring migrations, supporting the idea that Robins passing through northern Iberia migrated in short steps. In winter, however, higher values of body mass (but not of fat scores) were observed.

The European Robin *Erithacus rubecula* is a common Palaearctic songbird, breeding from west Iberia to the east Urals, and from northern Europe to North Africa, as well as in Ireland, Britain and Macaronesia (Cramp 1988, Mead 1997). Its migratory behaviour ranges from completely migratory in northern Europe to resident in southern Europe, with intermediate populations being partially migratory (Adriaensen & Dhondt 1984, Cramp 1988).

Iberia is one of the most relevant wintering quarters for a number of populations of Robins from west Europe (Bueno 1998, Tellería et al 2001a, Catry et al 2004). Information on migration and wintering of Robins in Iberia comes from three main sources: recaptures in Iberia of Robins ringed abroad (Bueno 1998), phenological data derived from systematic census (reviewed in Tellería et al 1999) and, finally, more-specific analyses on the features and interactions between foreign and local birds at their wintering areas (Tellería et al 2001b, Domínguez et al 2007). As a result, the general migration and wintering pattern for the species in Iberia is relatively well known, with the autumn migration period lasting from September to November, with a main peak in October, and the spring migration from February to April, with a peak in March. However, apart from these general data, detailed information about the migration and wintering behaviour of the species in given areas, including phenology, biometrics and sex and age ratios, is scarce. This becomes especially evident in northern Iberia, in spite of the fact that this is a region of obligate passage for many populations that overwinter in southern Iberia or Africa (Bueno 1998).

Our aim here was to describe in detail the migration and wintering of Robins at a site in northern Spain. In particular, we focused on seasonal patterns of (1) captures and the relationship between migrating and wintering Robins, (2) age and sex ratios, (3) biometrics, fuel load and body condition, and (4) flight ranges of Robins, estimated from fuel load.

## **METHODS**

#### Sampling area and ringing protocol

Data were collected at Plaiaundi Ecological Park (23.4 ha), situated near Bidasoa river mouth (Txingudi marshlands), Irún, N Spain (43°20'N 01°47'W). Vegetation in this area was characterised by a mosaic of woodlands (composed of an incipient Atlantic forest of oaks *Quercus* spp, and a riparian forest of alders *Alnus* spp), hedgerows (formed by willows *Salix*, tamarisk *Tamarix*, or Cantabrian hedgerow formed by species of genus *Rubus*, *Prunus*, *Cornus*, *Crataegus and Frangula*), grasslands, and reed beds *Phragmites australis*. Although Robins are common breeders in north Iberia

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(Galarza 1987, Purroy 2003), fewer than five pairs bred at Plaiaundi during the study (J. Arizaga pers. obs.), so the species was chiefly a migrating and wintering one in the study area.

Robins were mist-netted (72 m of nets placed in four linear sets) weekly (one session per week, normally on weekends) for 4 h from dawn, from July 2004 to May 2005. Sampling sessions were cancelled during rainfall. As Robins were trapped only between September and April, only data from this period have been considered here. Once captured, each bird was ringed and its age was determined using plumage features (Svensson 1998). Robins were classified either as first-winter (EURING code 3 or 5: Robins with retained juvenile feathers, caught after their partial post-juvenile moult) or adult (EURING code 4 or 6: Robins caught after their complete moult). We also recorded wing length (Method III of Svensson 1998, ± 0.5 mm), tail length ( $\pm 0.5$  mm), length of 8th primary feather (P8, numbered from proximal to distal,  $\pm 0.5$  mm), tarsus length ( $\pm 0.1$  mm), weight (Tanita digital balance,  $\pm 0.1$  g), breast muscle scores (scaled from 0 to 3,  $\pm$  0.5, Pinilla 2000) and fat scores (scaled from 0 to 8,  $\pm$  0.5, Kaiser 1993).

#### Sex determination

DNA analyses were used to determine the sex of Robins (Griffiths et al 1998, Gutiérrez-Corchero et al 2002). A sample of 0.05 to 0.10 ml of blood was taken from the jugular vein of living Robins (authorised by Diputación de Gipuzkoa). We stored each sample in a 1.5-ml vial, filled with 99% ethanol. Thereafter, we amplified the DNA sequence relative to the CHD-protein, present in both Z and W sex chromosomes, using the Polymerase Chain Reaction (PCR) technique. PCR fragments were separated by electrophoresis on a 2.5% agarose gel. Gels were observed under UV light, and photographed. According to Griffiths et al (1998), a single band of DNA on the gel is characteristic of males (corresponding to CHD-Z gene), whilst two bands are present in females (corresponding to both CHD-Z and CHD-W). Of the 185 Robins ringed, sex was determined for 172 (93%).

#### Data analysis

Data were pooled into monthly periods to describe phenological patterns of Robins at Plaiaundi Park, since a smaller study unit would reduce the sample size too much. The number of sampling sessions ranged from three to five a month, and abundance was expressed as the mean number of Robins caught per sampling day. Proportions of age and sex categories were analysed using tests based on chi-square ( $\chi^2$ ) values. The *P*-exact value was used when more than 25% of expected values were <5, or in 2×2 tables (Agresti 1996).

Biometric differences in relation to age, sex and time (months) were analysed with Univariate Linear Models (ULM). A ULM with all these factors would have diminished the sample size too much in some months, so the analysis was developed in two steps. Firstly, we ran a two-way ANOVA on biometric variables (wing, tail, P8 and tarsus length) and age and sex as factors (for all variables, the data conformed to statistical assumptions for parametric tests). Thereafter, residuals of the two-way ANOVAs (*ie* each variable once the age and sex effects were removed; Alonso *et al* 2006) were analysed in an ANOVA with month as factor.

In addition, a stepwise Discriminant Function Analysis (DFA) was used to separate the sexes on the basis of biometric data. Since these measurements did not differ between age classes (see results for further details), the two age classes were pooled for analysis.

Body condition was estimated with (1) body mass in relation to body size (assessed here with wing length; Gosler et al 1998), (2) fuel load over lean body mass (body mass without any visible fat content), (3) breast muscle scores, and (4) fat scores. Note that body mass in a bird is the sum of structural mass (skeleton, feathers and organs), proteins (ie muscle mass) and fat stores. Thus, although body mass in relation to body size (this last mainly correlated with structural mass and mass due to proteins) provides a good estimation of fuel load stored as fats (most fuel in a bird is stored as lipids; Jenni & Jenni-Eiermann 1998), it also includes to some extent some mass stored as non-fat. Similarly, lean mass (used to calculate fuel load over lean body mass, as shown below) is defined as body mass in birds without any visible fat content, but it is also possible that such birds have fuel available which is stored as proteins.

Both body mass and fuel load over lean body mass fitted the normal distribution, so parametric procedures were used in this case (a ULM with months as factor). Timedependent variation in muscle and fat scores were analysed with Kruskal–Wallis tests.

To estimate fuel load over lean body mass we followed the equation:

#### $FL = [(ABM - LBM) / LBM] \times 100$

where FL is fuel load, ABM is actual body mass and LBM is lean body mass. LBM was obtained from regressing ABM on wing length for those birds without any visible fat content (fat = 0); ABM = (0.352 × wing length) – 9.784 (r = 0.678,  $F_{1,11}$  = 8.531, *P* = 0.015, N = 12). Negative FL were considered to be zero. Most (75%) of the Robins used to estimate this function were captured in autumn.

As reviewed by Weber & Houston (1997), flight ranges can be estimated by two main different procedures: with models deduced from analyses of measured cost of flight or with those based on aerodynamics. Since the former models can report ranges differing by an order of magnitude, using the latter type is more conservative. Therefore, to estimate flight ranges in relation to fuel load of Robins at Plaiaundi we used the Flight software v1.17 (Pennycuick 1989, 1998). The following parameters were introduced into the model: fuel load over lean body mass, zero crop mass, 0.2 m of wing span, 0.0076 m<sup>2</sup> of wing area (J. Arizaga unpubl. data), flying at 1,000 m asl (Alerstam & Lindström 1990), under still air conditions for this altitude (8.5°C, 898 hPa, 1.11 kg.m<sup>-3</sup>; Pennycuick 1989, 1998).

Statistics were calculated with SPSS v15.0 for Windows and means are given  $\pm$  SE.

#### RESULTS

#### Seasonal patterns of abundance and proportion of recaptures

From September 2004 to April 2005, 185 Robins were captured; 24 of these were recaptured on 47 occasions, resulting in 232 capture events overall. No recaptures from elsewhere were obtained. Robins first appeared at Plaiaundi Park by mid September (Fig 1). A peak in abundance occurred by October and the number of captures thereafter declined progressively to February (from 21.6 captures/day in October to 2.0 captures/day in February). A new peak was observed in March, although much smaller than that registered in October (21.6 captures/day in October versus 6.7 captures/day in March), and very few Robins were caught by April. Recaptures increased from October to January (50% in January, Fig 1), decreasing thereafter to zero by April. Most Robins (ringed in September or subsequently) were recaptured between October and January, whereas only two (12.5%) were recaptured in February, and one in March (6.3%). Some Robins captured in September and October (N = 6) were recaptured once or more during winter (December and January), supporting the notion of resident winter visitors.



**Figure 1.** Seasonal patterns of captures (mean number of captures per day; open bars) and proportion of recaptures (percentage; dots) of Robins at the Plaiaundi Park, a locality in N Spain, during 2004–05.

#### Age and sex ratios

Robins identified as first-winter (mean from September to April, 86.0%) were always more abundant than adults ( $\chi^{2}_{1}$  = 95.616, *P*-exact < 0.001). This proportion varied during the study period ( $\chi^{2}_{7}$  = 17.017, *P*-exact = 0.022; Fig 2). Overall, females were more abundant than males (69.2%;  $\chi^{2}_{1}$  = 25.326, *P*-exact < 0.001), but the sex ratio also varied seasonally ( $\chi^{2}_{7}$  = 13.997, *P*-exact = 0.046; Fig 2). However, *a posteriori* paired comparisons for age and sex ratios did not demonstrate significant differences, and this is likely to be a result of the low sample sizes for some sampling periods.

#### **Biometrics**

Morphological traits varied only between sex classes and not between ages, with males having longer wings, tails



**Figure 2.** Seasonal patterns of variation of (a) age and (b) sex proportions. Within each case, proportion of Robins of a particular age or sex class was given, with all other birds assigned to the other class. Sample sizes are shown for each month above each figure.

and P8 (Tables 1 & 2; each bird considered only once). A stepwise DFA showed that only wing length was useful for separating the sexes (Wilks'  $\lambda = 0.589$ , P < 0.001, 83.1% of cases correctly classified). From an empirical viewpoint, the overlap between sexes is important (Fig 3) and the sex ratio was around 1:1 for birds with wings between 73.0 and 73.5 mm. Conversely, birds with a wing  $\geq$  75.0 mm were always males and those with  $\leq$  69.5 mm were always females (Fig 3).

Once sex effects were removed (each bird considered only once a month), only wing length varied during the study period (residual wing length:  $F_{7,194} = 2.170$ , P = 0.039; residual tail length:  $F_{7,192} = 1.416$ , P = 0.201; residual tarsus length:  $F_{7,194} = 2.032$ , P = 0.053; residual P8:  $F_{7,194} = 1.681$ , P = 0.116). A Tukey B test (pairwise comparisons) revealed that variations in wing length were due to data from April, but the low sample size then precluded firm conclusions about these differences.

#### Body mass, fat levels and flight ranges

For this analysis, each bird was considered once a month and birds with missing biometric data were removed. Body mass ranged from 13.5 to 22.8 g (mean = 16.4 ± 0.1 g, N = 204), and varied during the study period ( $F_{7,203} = 5.864$ , P < 0.001; wing length:  $F_{7,203} = 18.998$ , P < 0.001), with a peak by January (Fig 4). Estimated fuel load varied from 0 to 43.3% over lean body mass (mean = 6.6% ± 0.6 , N = 204), and was also observed to change during the study period ( $F_{7,203} = 5.784$ , P < 0.001), with a peak by January (Fig 4). In contrast, neither muscle (mean = 1.6 ± 0.1, N = 204; K–W test:  $H^2_7 = 4.800$ , P = 0.684) nor fat scores varied with time (mean = 1.6 ± 0.1, N = 204; K–W test:  $H^2_7 = 5.038$ , P = 0.655; Fig 4).

As estimated fuel load varied during the study period (Fig 4), possible flight ranges also varied. For Robins caught from September to November (potential autumn migration) their apparent fuel load would allow them to cover, under still air conditions, a distance of around 400

**Table 1.** Biometrics of Robins caught at Plaiaundi from September2004 to April 2005, in relation to age and sex classes.

Length (mm)	First-wir Males	nter Females	Adult Males	Females	
Wing	73.9 ± 0.2	71.2 ± 0.2	74.9 ± 0.8	71.3 ± 0.4	
	(N = 47)	(N = 100)	(N = 6)	(N = 19)	
Tail	61.1 ± 0.1	58.9 ± 0.2	61.6 ± 1.2	59.4 ± 0.4	
	(N = 47)	(N = 98)	(N = 6)	(N = 19)	
Tarsus	25.3 ± 0.1	25.0 ± 0.1	25.5 ± 0.1	25.3 ± 0.1	
	(N = 47)	(N = 100)	(N = 6)	(N = 19)	
P8	56.3 ± 0.2	54.0 ± 0.1	56.5 ± 1.0	53.2 ± 0.9	
	(N = 47)	(N = 100)	(N = 6)	(N = 19)	

km without needing to refuel. Between December and January, however, flight ranges estimated on the basis of these apparent fuel loads were higher (nearly 1,000 km in January). Finally, Robins caught from February to April had sufficient fuel loads for flights of up to 400 km, although this figure should be treated with caution, due to the low sample size, especially in April.

## DISCUSSION

Robins occurred at Plaiaundi during eight months a year, from September to April, agreeing with data of Bueno (1998) and Tellería *et al* (1999) for migrating and wintering Robins in Spain. The seasonal patterns of abundance and proportion of recaptures suggest three phenological phases: autumn migration period (from September to November, with a peak in October), spring migration period (March and April, with a peak in March) and wintering (from December to February).

No measures of body size varied during the study period, so, in this respect, Robins that overwintered at Plaiaundi were similar to those passing through. In contrast, body mass, controlled for body size, and fuel load over lean body mass, but not fat nor muscle scores, varied with time.

#### Autumn migration period

From September to November, new captures were abundant, but the proportion of recaptures was low. A peak of captures in October agrees with other data for all Iberia (Bueno 1998, Tellería *et al* 1999) and, more particularly, with data reported from northern (Galarza 1987, Grandío & Belzunce 1990) and southern Iberia



Figure 3. Distribution of wing length) for each sex category. Sample size: females, N = 119; males, N = 53.

	Wi	Wing		Tail		Tarsus		P8	
	F <sub>1,171</sub>	P	F <sub>1,169</sub>	Р	F <sub>1,171</sub>	Р	F <sub>1,171</sub>	Р	
Age	3.630	0.058	1.513	0.220	1.493	0.223	0.359	0.550	
Sex	60.11	<0.001	25.03	<0.001	1.597	0.208	31.64	<0.001	
Age × Sex	0.464	0.497	0.005	0.945	0.130	0.719	0.876	0.251	

Table 2. Two-way ANOVAs on biometrics of Robins at Plaiaundi in relation to age and sex.

(Murillo & Sancho 1969, Tellería 1981). This passage between September and November with a peak in October is also similar to that observed in the Italian Alps (Bottoni *et al* 1991). As expected for its more northerly latitude, the peak of migration in northern Europe occurs in September (Högstedt & Persson 1971, Roos 1984).

In autumn, Robins captured were mainly first-winter (>85%). Similar results were reported by Murillo & Sancho (1969) in Doñana (southwest Iberia), probably since adult birds remain close to their breeding areas (Tellería & Pérez-Tris 2004). However, Tellería *et al* (2001a) observed that, even among local birds, first-winter birds were more abundant than adults, irrespective of habitat.

Females were the more abundant sex, amounting to more than 70% of captures. In Belgium, Adriaensen & Dhondt (1990) found that local wintering birds were mainly males. By contrast, as at Plaiaundi, in southwest Iberia, Catry *et al* (2004) reported that the majority of Robins during the winter were females. Thus, together with the fact that most of the Robins passing through Plaiaundi were females, these observations suggest differential migration distances according to sex for the west European populations.

Overall, both body mass and apparent fuel load in autumn were lower than during the winter. Thus, with a mean body mass of 16.2 g in October, at the peak of migration, Robins stopping over at Plaiaundi would be able to cover a distance of up to 300 km under still air conditions, without needing to refuel. This body mass (equivalent to a fuel load between 5% and 10%) contrasts with the higher fuel load reported for the majority of migrating passerines wintering in temperate latitudes (between 15% and 25%; Alerstam & Lindström 1990). In Robins captured during the autumn migration period in northern Europe, the mean fuel load was around 50% (Dänhardt & Lindström 2001), in contrast to the maximum of about 20% seen at Plaiaundi. These results suggest that European Robins do not put on much fuel when they migrate through Iberia, and have a migration strategy based on many short steps, rather than on fewer long-distance flights. This has been also proposed for other small thrushes, such as Bluethroats Luscinia svecica, when crossing Iberia (Bermejo & De la Puente 2004). It is also possible that a number of Robins ringed at Plaiaundi in autumn could spend the winter near this site. In this case, the lower body mass and fuel load would reflect their arrival near their wintering areas (Berthold 2001).

## Wintering

The winter period lasted from December to February, and was characterised by few new captures and a high proportion of recaptures (more than 40%). The number of captures may seem lower than in other areas in south Iberia (which have a higher number of Robins in winter; Tellería et al 1999,- but see Murillo & Sancho 1969), though we have no comparable data from standardised ringing studies in southern Iberia. To explain this result at Plaiaundi, two non-exclusive hypotheses are proposed. First, that the number of Robins wintering in northern Iberia is low compared with southern Iberia (Tellería et al 2001b), since the availability of fruits and insects in northern Iberia is comparatively poorer during the winter (Herrera 1985, Fuentes 1992). Second, Robins may show territorial behaviour in winter (Adriaensen & Dhondt 1990, Cuadrado 1997, Tellería et al 2001a), so those birds established near net sites would be more likely to be captured than Robins with territories away from nets. This is supported by the high proportion of recaptures during the winter (almost 50% in January).

Some of the Robins overwintering at Plaiaundi were captured as early as September, before the autumn peak of migration. This suggests that at least some of the initial arrivals at Plaiaundi in autumn have a high probability of overwintering in the area. The mechanisms that regulate this phenomenon may be associated with patterns of dominance: birds arriving early would be able to occupy the best feeding territories and defend them against birds arriving later. However, it is also possible that some wintering birds may arrive later and that, because of their dominant status, could displace Robins already present.

In contrast to this pattern, most wintering individuals seemed to leave the study area before the spring peak in March, when the number of recaptures decreased. Thus, the overlap between wintering and migrating Robins in spring was probably low. This is consistent with a general migratory pattern for birds to leave their wintering areas early, so as to reach breeding areas in spring as soon as possible (eg Stewart et al 2002). Accordingly, Tellería et al



**Figure 4.** Seasonal patterns of body condition variation, measured as body mass (corrected for body size), fuel load over lean body mass, and fat and muscle scores. Sample size, in brackets. Flight ranges are shown above. In the first two cases, months with the same letters are those for which no significant differences were detected with an *a posteriori* test.

(1999) reported that breeding quarters in Iberian mountain ranges were occupied by Robins as early as March.

Overall, the high proportion of first-winter Robins at Plaiaundi is in agreement with data for habitats where Robins tend to occur only outside the breeding season (Figuerola *et al* 2001, Catry *et al* 2004, but see Tellería *et al* 2001a). The proportion of adult Robins tended to increase to 40% during September to February. In southern Iberia, Murillo & Sancho (1969) also reported an increasing proportion of adult birds (up to 45.5%) in winter. This phenomenon can be explained by two nonexclusive hypotheses. First, it could be due to different survival rates between age classes (Adriaensen & Dhondt 1990, Venticinque & Consiglio 1993), for example if adult birds had a higher foraging efficiency (Moore *et al* 2003) or were able to occupy and defend better feeding territories (Carpenter *et al* 1993, Tellería *et al* 2001a, Moore *et al* 2003). This needs to be investigated by survival analyses of wintering Robin populations. Second, new adult birds might arrive at Plaiaundi in midwinter, when adverse weather at wintering areas further north might force them to move to more suitable places.

Both body mass and the apparent fuel load had higher values in winter, with a peak in December (around 15% of fuel over lean mass). Interestingly, fat and muscle scores did not vary significantly during the winter. Robins used to estimate lean mass were captured mainly in autumn; thus, if they had muscle scores lower than wintering ones, the fuel load of Robins captured during winter would be overestimated. However, flight muscle scores were constant along the whole study period, so this hypothesis is incorrect unless proteins (or additional mass) are stored in other tissues apart from flight muscle (Piersma & Jukema 2002). Alternatively, it is possible that fat scores are not sufficiently accurate to detect biologically significant differences in fuel load, compared to estimating fuel load from the excess over lean body mass (Kaiser 1993). Indeed, the mean difference in body mass between autumn and winter was  $\leq 2$  g. Moreover, it cannot be excluded that part of the fuel load is stored as proteins (muscle mass), rather than just fats (Jenni & Jenni-Eiermann 1998). It is noteworthy that some species tend to gain mass as fats during autumn, but as proteins before the spring migration period (Piersma & Jukema 2002). Clearly, there is a lack of information on how birds change their body composition between seasons, and, as seems most relevant, how this may affect the estimation of fuel load and flight ranges in migrants.

#### Spring migration period

The spring migration spanned March to April, although the number of captures in April was very low, suggesting that most Robins had passed through the area by March. As reported in other areas in Spain (Murillo & Sancho 1969, Tellería 1981, Galarza 1987, Grandío & Belzunce 1990; reviewed by Tellería *et al* 1999), the peak spring migration was in March and conforms to the general pattern for Iberia (Bueno 1998). In northern Italy (Bottoni *et al* 1991) and in northern Europe (Högstedt & Persson 1971, Roos 1984), the spring migration period is reported to be from April to May. Captures at Plaiaundi in March were a quarter those in October and the phenomenon of a less conspicuous spring migration period has been reported for Robins in other zones of Iberia (reviewed by Tellería *et al* 1999); this is also common in other migrating passerines in spring (Berthold 2001) and has been linked to the maintenance of higher migratory speeds, shorter stopover durations, and fewer stopover events compared with autumn. In addition, Robins passing through Plaiaundi (west Pyrenees) in autumn could use other routes in spring, as reported for other species (reviewed by Bairlein 2001).

It is also possible that some of the Robins captured in March could be birds arriving near breeding areas in northern Iberia or southwest France. Both body mass and fuel load over lean mass were lower during spring than during winter, although similar to autumn birds. Therefore, Robins stopping over at Plaiaundi may be moving in short steps to their next goal areas further north, or may be birds heading for adjacent breeding areas. Considering both autumn and spring migrations together, the ringing data suggest that Robins at Plaiaundi are either birds moving short distances (breeding and wintering close to the study site), or moving longer distances but migrating in relatively short steps. Studies to distinguish these possibilities will be important for understanding the population biology of Robins in Iberia.

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## REFERENCES

- Adriaensen, F. & Dhondt, A.A. (1984) Dynamics of a Robin population outside the breeding season. Bird Study 31, 69–75.
- Adriaensen, F. & Dhondt, A.A. (1990) Territoriality in the continental European robin, Erithacus rubecula rubecula. Ardea 78, 459–465.

- Agresti, A. (1996) An introduction to categorical data analysis. Wiley Interscience, New York.
- Alerstam, T. & Lindström, A. (1990) Optimal bird migration: the relative importance of time, energy and safety. In *Bird Migration: Physiology and Ecophysiology* (ed Gwinner, E.), pp 331–351. Springer-Verlag, Berlin.
- Alonso, D., Arizaga, J., Miranda, R. & Hernández, M.A. (2006) Morphological diversification of Common Crossbill *Loxia curvirostra* populations within Iberia and the Balearics. *Ardea* 94, 99–107.
- Bairlein, F. (2001) Results of bird ringing in the study of migration routes. Ardea 89, 7–19.
- Bermejo, A. & De la Puente, J. (2004) Wintering and migration of Bluethroat (*Luscinia svecica*) in central Spain. Ardeola 51, 285–296.
- Berthold, P. (2001) Bird migration: a general survey. Oxford University Press, Oxford.
- Bottoni, L., Massa, R. & Fornasari, L. (1991) The migration of the Robin Erithacus rubecula in the central Pre-Alps of Italy. *Ringing & Migration* 12, 48–53.
- Bueno, J.M. (1998) Migración e invernada de pequeños turdinos en la Península Ibérica. V. Petirrojo (*Erithacus rubecula*). Ardeola 45, 193–200.
- Carpenter, F.L., Hixon, M.A., Russel, R.W., Paton, D.C. & Temeles, E.J. (1993) Interference asymmetries among age-classes of rufous hummingbirds during migratory stopover. *Behavioural Ecology* and Sociobiology **33**, 305–312.
- Catry, P., Campos, A., Almada, V. & Cresswell, W. (2004) Winter segregation of migrant European robins *Erithacus rubecula* in relation to sex, age and size. *Journal of Avian Biology* **35**, 204–209.
- Cramp, S. (ed) (1988) Handbook of the Birds of the Europe, the Middle East and North Africa. Volume V. Oxford University Press, New York.
- Cuadrado, M. (1997) Why are migrant Robins (Erithacus rubecula) territorial in winter?: the importance of the anti-predatory behaviour. Ethology, Ecology and Evolution 9, 77–88.
- Dänhardt, J. & Lindström, Å. (2001) Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. Animal Behaviour 62, 235–243.
- Domínguez, M., Barba, E., Cantó, J.L., López, G.M. & Monrós, J.S. (2007) Seasonal interchange of European robin Erithacus rubecula populations in an evergreen oak forest. Acta Ornithologica 42, 15–21.
- Figuerola, J., Jovani, R. & Sol, D. (2001) Age-related habitat segregation by robins *Erithacus rubecula* during the winter. *Bird Study* 48, 252–255.
- Fuentes, M. (1992) Latitudinal and elevational variation in fruit phenology among Western European bird-dispersed plants. *Ecography* 15, 177–183.
- Galarza, A. (1987) Seasonal description of passerine communities in a coastal farm-land of the Basque Country. *Munibe* 39, 3–8.
- Gosler, A.G., Greenwood, J.J.D., Baker, J.K. & Davidson, N.C. (1998) The field determination of body size and condition in passerines: a report to the British Ringing Committee. *Bird Study* 45, 92–103.

- Grandío, J.M. & Belzunce, J.A. (1990) Seasonal structure of the passerine communities in a marsh of the Atlantic Basque Country. *Munibe* 41–42, 47–58.
- Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. (1998) A DNA test to sex most birds. *Molecular Ecology* 7, 1071–1075.
- Gutiérrez-Corchero, F., Arruga, M.V., Sanz, L., García, C., Hernández, M.A. & Campos, F. (2002) Using FTA cards to store avian blood samples for genetic studies: their application in sex determination. *Molecular Ecology Notes* 2, 75–77.
- Herrera, C.M. (1985) Habitat–consumer interaction in frugivorous birds. In *Habitat selection in birds* (ed Cody, M.L.), pp 341–365. Academic Press, London.
- Högstedt, G. & Persson, C. (1971) Phånologie und Überwinterung der über Falsterbo ziehenden Rotkehlchen. Vogelwarte 26, 86–98.
- Jenni, L. & Jenni-Eiermann, S. (1998) Fuel supply and metabolic constraints in migrating birds. *Journal of Avian Biology* 29, 521– 528.
- Kaiser, A. (1993) A new multicategory classification of subcutaneous fat deposits of songbirds. *Journal of Field Ornithology* 64, 246–255.
- Mead, C. (1997) Erithacus rubecula Robin. In The EBCC Atlas of European Breeding Birds (eds Hagemeijer, W.J.M. & Blair, M.J.), pp 512–513.
  T. & A.D. Poyser, London.
- Moore, F., Mabey, S. & Woodrey, M. (2003) Priority access to food in migratory birds: age, sex and motivational asymmetries. In *Avian migration* (eds Berthold, P., Gwinner, E. & Sonnenschein, E.), pp 281–292. Springer-Verlag, Berlin.
- Murillo, F. & Sancho, F. (1969) Migración de Sylvia atricapilla y Erithacus rubecula en Doñana según datos de capturas. Ardeola 13, 129–137.
- Pennycuick, C.J. (1989) Bird flight performance: a practical calculation manual. Oxford University Press, Oxford.
- Pennycuick, C.J. (1998) Computer simulation of fat and muscle burn in long-distance bird migration. *Journal of Theoretical Biology* 191, 47–61.

- Piersma, T. & Jukema, J. (2002) Contrast in adaptive mass gains: Eurasian golden plovers store fat before midwinter and protein before prebreeding flight. *Proceedings of the Royal Society of London Series* B 269, 1101–1105.
- Pinilla, J. (ed) (2000) Manual para el anillamiento científico de aves. SEO/BirdLife-DGCN-MIMAM, Madrid.
- Purroy, F.J. (2003) Petirrojo Erithacus rubecula. In Atlas de las aves reproductoras de España (eds Martí, R. & del Moral, J.C.), pp 416–417. DGCN–SEO/BirdLife, Madrid.
- Roos, G. (1984) Flyttning, övervintring och livslängd hos fåglar ringmärkta vid Falsterbo (1947–1980). Anser Suppl. 13.
- Stewart, R.L.M., Francis, C.M. & Massey, C. (2002) Age-related differential timing of spring migration within sexes in passerines. *Wilson Bulletin* 114, 264–271.
- Svensson, L. (1998) Guía para la identificación de los paseriformes. SEO/Birdlife, Madrid.
- Tellería, J.L. (1981) La migración de las aves en el Estrecho de Gibraltar. Volume 2. Aves no planeadoras. Universidad Complutense, Madrid.
- Tellería, J.L. & Pérez-Tris, J. (2004) Consequences of the settlement of migrant European Robins *Erithacus rubecula* in wintering habitats occupied by conspecific residents. *Ibis* 146, 258–268.
- Tellería, J.L., Asensio, B. & Díaz, M. (1999) Aves Ibéricas. II. Paseriformes. J.M. Reyero, Madrid.
- Tellería, J.L., Pérez-Tris, J. & Carbonell, R. (2001a) Seasonal changes in abundance and flight-related morphology reveal different migration patterns in Iberian forest passerines. Ardeola 48, 27–46.
- Tellería, J.L., Pérez-Tris, J., Ramírez, A., Fernández-Juridic, E. & Carbonell, R. (2001b) Distribution of robins *Erithacus rubecula* in wintering grounds: effecs of conspecific density, migratory status and age. *Ardea* 89, 363–373.
- Venticinque, L. & Consiglio, C. (1993) Winter density of the robin Erithacus rubecula in central Italy. Alauda 61, 52–54.
- Weber, T.P. & Houston, A.I. (1997) A general model for timeminimising avian migration. *Journal of Theoretical Biology* 185, 447–458.

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