

Differential migration of chiffchaffs *Phylloscopus collybita* and *P. ibericus* in Europe and Africa

Paulo Catry, Miguel Lecoq, António Araújo, Greg Conway, Marcial Felgueiras, J. Michael B. King, Stephen Rumsey, Hamidi Salima and Paulo Tenreiro

Catry, P., Lecoq, M., Araújo, A., Conway, G., Felgueiras, M., King, J. M. B., Rumsey, S., Salima, H. and Tenreiro, P. 2005. Differential migration of chiffchaffs *Phylloscopus collybita* and *P. ibericus* in Europe and Africa. – *J. Avian Biol.* 36: 184–190.

Differential migration is a widespread, but poorly understood, phenomenon in birds. In this paper, we present the first detailed field study of differential migration in the Old World warbler (Sylviidae) family. We studied two chiffchaff *Phylloscopus [collybita]* semispecies: the common chiffchaff *P. [c.] collybita* and the Iberian chiffchaff *P. [c.] ibericus*. Using data collected at several latitudes in Europe and Africa, we present convincing evidence for differential distance migration of sexes in chiffchaffs, with females moving further than males. Interestingly, while there was a pronounced gradient in the sex-ratios in Europe and North Africa (with an increasing proportion of females with declining latitude), no clear pattern was found south of the Sahara, where sex-ratios were more male-biased than predicted by a simple latitude model. This suggests that, amongst the chiffchaffs wintering in West Africa, a large proportion is composed by Iberian birds, and provides support to previous suggestions that Iberian chiffchaffs are long distance migrants. Results from detailed studies in Senegal also show that chiffchaffs display differential timing of spring migration, with males leaving the winter quarters considerably earlier than females. The results are discussed in the framework of the three main (non-mutually exclusive) hypotheses attempting to explain the latitudinal segregation of the sexes. Given the relative failure of standard comparative studies to discriminate between competing single-factor hypotheses to explain differential migration, it is argued that the chiffchaff species complex might be particularly suited to study this issue using a new approach suggested by Cristol et al. (1999): detailed (further) comparisons between closely related species (such as the common and the Iberian chiffchaffs) could help identifying the key factors to be incorporated into optimality models that can predict relative distance of migration of different sex or age classes.

P. Catry (correspondence), Unidade de Investigação em Eco-Etologia, Instituto Superior de Psicologia Aplicada, Rua Jardim do Tabaco 44, 1100 Lisboa, Portugal. E-mail: paulo.catry@netc.pt. M. Lecoq, Sociedade Portuguesa para o Estudo das Aves, Rua da Vitória n.º 53 – 3 esq., 1100, Lisboa, Portugal. A. Araújo, Parc National du Banc d'Arguin, BP 4249, Nouakchott, Mauritanía. G. Conway, British Trust for Ornithology, Nunnery Place, Thetford, Norfolk, IP24 2PU, UK. M. Felgueiras, A Rocha, Centro de Estudos Cruzinha, Quinta da Rocha, Apartado 41, 8501-903, Mexilhoeira Grande, Portugal. S. Rumsey, The Wetlands Trust, Elms Farm, Pett Lane, Icklesham, Winchelsea, East Sussex TN 36 4AH, UK. H. Salima, Laboratoire d'Hydrobiologie et Ecologie Générale, Faculté des Sciences, Université Mohamed Premier, BP 524. Oujda, Morocco. P. Tenreiro, Instituto da Conservação da Natureza, Mata Nacional do Choupal, 3000, Coimbra, Portugal.

Differential migration is said to occur when different classes of individuals (for example different age or sex-classes) display differences in timing and length of the

migratory movements. Differential migration is an interesting phenomenon, particularly because its study could contribute to shed light on the evolution of

migration in general (Ketterson and Nolan 1983). One consequence of differential distance migration is the geographical segregation of classes of individuals in the winter quarters, which can have important implications for both population dynamics and conservation (Sherry and Holmes 1996, Rodenhouse et al. 1997, Catry et al. 2005).

Three main hypotheses have been presented to account for the differential distance migration of sexes (Cristol et al. 1999 for a recent review). (1) The body-size (or cold-tolerance) hypothesis suggests that the winter segregation is linked to the differential resistance to cold weather of differently sized classes. Briefly, smaller individuals should preferably winter in milder climates and larger ones can remain in harsher environments, closer to the breeding grounds (Ketterson and Nolan 1976). (2) According to the dominance hypothesis, subordinate individuals are forced to move to areas further away from the breeding grounds by the dominant classes, which tend to move shorter distances or remain sedentary (Gauthreaux 1982). (3) The arrival-time hypothesis states that individuals under greater pressure to outrun potential competitors, in the timing of arrival to the breeding grounds, should have a greater benefit from wintering closer to the nesting areas (Ketterson and Nolan 1976, Myers 1981). These three hypotheses are not mutually exclusive, which makes them particularly hard to test and refute.

Differential migration of the sexes has been demonstrated in many bird species from various phylogenetic and ecological groups (Cristol et al. 1999). This subject has been little studied in the large (and mostly migratory) family of the Old-World warblers (Sylviidae), and no species has been conclusively shown to be a differential (distance) migrant (Cristol et al. 1999). In their recent review, Cristol et al. (1999) presented the blackcap *Sylvia atricapilla* as a probable differential migrant. However, laboratory evidence of differential migratory behaviour in this species has yielded contradictory results (Terril and Berthold 1989, Berthold and Pulido 1994).

In this paper, we compile data from several original field studies, in Europe and Africa, to investigate the geographical segregation by sex of another Old World Warbler, the chiffchaff *Phylloscopus [collybita]*. The superspecies *Phylloscopus [collybita]* (hereafter called chiffchaff) includes the semispecies common chiffchaff *P. collybita* and the Iberian chiffchaff *P. ibericus* (Helbig et al. 2002, see also Svensson 2001, Knox et al. 2002, Salomon et al. 2003). Common chiffchaffs of the nominate race (*P. c. collybita*; studied here) nest in the middle-latitudes of central and western Europe and winter chiefly in southwestern Europe, around the Mediterranean and in West Africa, south to the forest belt (Zink 1973, Cramp 1992). It seems likely that the Iberian chiffchaff is a long-distance migrant that winters

primarily in tropical Africa (Svensson 2001, Pérez-Tris et al. 2003), but definite proof is still lacking. Both semispecies are likely to be present south of the Sahara, in winter. Unfortunately, these cannot be easily told apart, and only recently (after the fieldwork supporting the present paper) apparently reliable discriminant criteria were developed (Svensson 2001).

In this paper, we present data on the sex-ratio composition of chiffchaff populations wintering at various latitudes in Europe and Africa. We test the hypothesis that male and female chiffchaffs have different winter distributions, and the hypothesis that they differ in their timing of spring migration. Although such data alone are not sufficient to conclusively support or reject any of the main hypotheses for differential migration in birds, they are necessary as a base to further study of this subject.

Methods

Fieldwork

We trapped chiffchaffs using mist-nets at several locations in the United Kingdom, Portugal, Morocco, Mauritania, Senegal and Gambia. To complete these data sets, we contacted national ringing centres and individual ringers asking for chiffchaff biometric data collected in winter, and succeeded in getting further data for other Portuguese sites and for France. We only used ringing data collected between 15 November and 31 January to avoid including birds that were caught during the main migratory periods of these species (Cramp 1992).

We always tried to confirm that birds used in our analyses had been trapped without recourse to tape-lures, because these are known to produce male-biased samples in this species (Lecoq and Catry 2003). Confirmation of no use of tape-lures was obtained for all samples involving a large number (>20) of individuals. However, confirmation could not be obtained from all ringers that contributed with data for the Portuguese and French chiffchaff data sets. Given that these ringers caught only small numbers of birds, it seems most unlikely that more than a small minority of them would have used tape-lures, which would make a small contribution to the overall data sets. At some sites (e.g. Djoudj, Senegal), tape lures were used in some occasions, but not in others. Only birds caught on periods without tape-luring were included.

Study areas

Chiffchaffs were trapped in the following locations: 1) United Kingdom. Mostly in southern England (particu-

larly in Cornwall), in sewage treatment works. Captures made in 1999–2000. 2) France. At various mainland locations in the Atlantic and Mediterranean coasts, and also inland (particularly in the South). No habitat details were obtained from the large number of trapping locations involved (data made available by the CRBPO Ringing Scheme). Captures made in 1990–2002. 3) North Portugal. At various locations in coastal areas south to the Mondego Valley, mostly in wetland margins (data made available by the ICN Ringing Scheme). Captures made in 1995–2001. 4) Central Portugal. At two main locations around Lisbon, at an estuary edge (Catry et al. 2003) and at Mediterranean scrubland habitats. Captures made in 1995–1999. 5) Southeast Portugal. At several locations in eastern Algarve, including diverse habitats such as pine woodlands, olive groves, orchards, open farmland and wetland margins. Captures made in 1990–1996. 6) Southwest Portugal. At mostly one location in western Algarve, near the Alvor estuary, in dry land covered with scrub and orchards. Captures made in 1995–2002. 7) Morocco. At one location, 8 km from Saïdia, in riparian vegetation dominated by tamarisks *Tamarix* sp. and several reed and rush formations. Captures made in 1995–1996. 8) Mauritania. At the artificial oasis formed by the city of Nouakchott, in the southern Sahara, in a small area with vegetable gardens. Captures made in 2001–2004. 9) Senegal. At the Doudj National Park, in the lower Senegal river. In reedbeds and other riparian vegetation as well as in scrubland and savanna (Sauvage et al. 1998 for more details on this site). Captures made in 1987–1996. 10) Gambia. At Ginak Island, at the mouth of the Gambia River, covered with savanna (where most ringing took place) and mangrove (Hjort et al. 1996 for more details). Captures made in 1994–2000.

The latitude of the wintering sites was either directly read from a map (for single locations), or estimated as a weighed mean of the latitudes of several locations within a region.

Sexing chiffchaffs

Chiffchaffs are sexually dimorphic with respect to wing-length (males larger) and there is little overlap between the sexes (Ticehurst 1938, Geen 1988, Salomon et al. 2003). We used a maximum likelihood mixture model to separate the strongly bimodal distributions of wing-lengths. Mixture models are routinely used in fisheries research to separate sex and age classes (e.g. MacDonald and Pitcher 1979). We used program MIX3.1a (© 1995 Ichthus Data Systems) to estimate the proportion of males in each chiffchaff sample and associated standard errors.

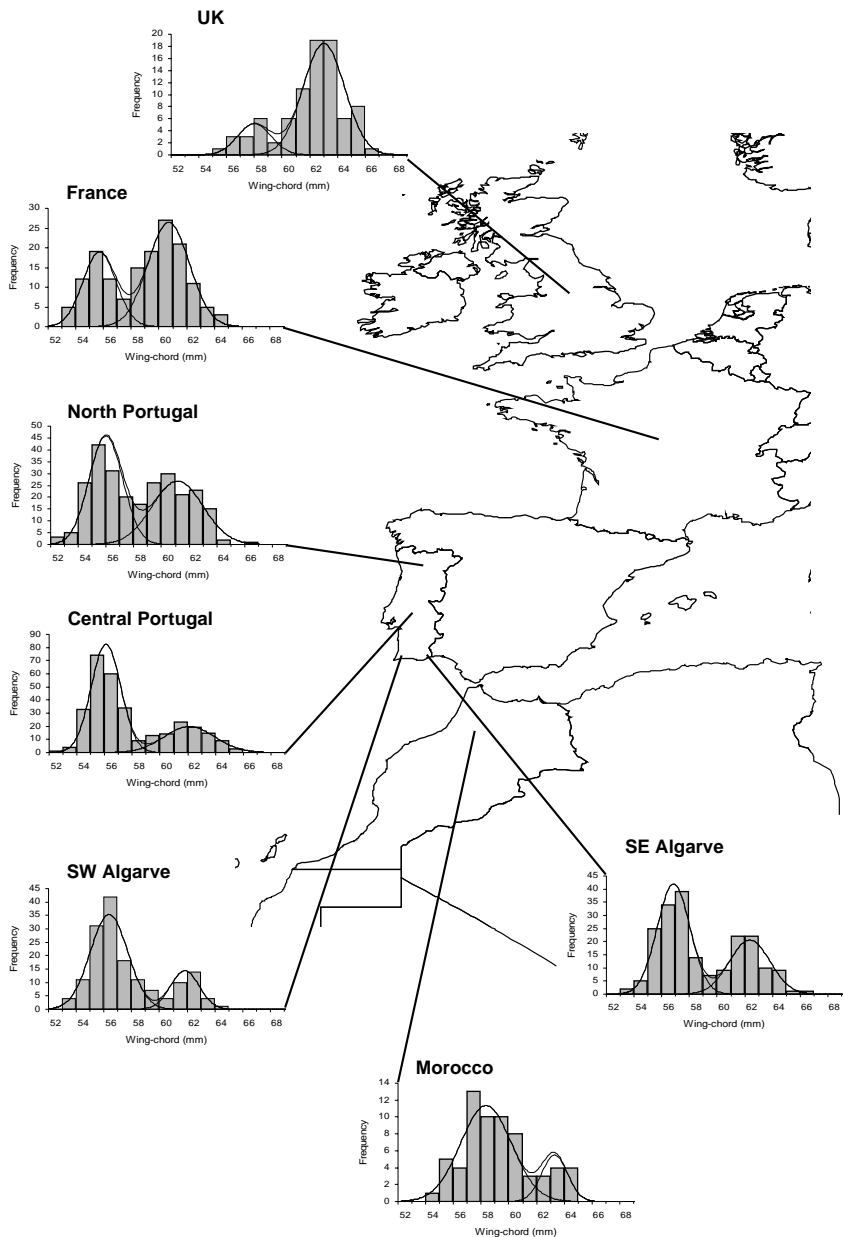
Although adult chiffchaffs have slightly longer wings than juveniles, as found in most passerines, we did not attempt to include this parameter in the mixture models or to do separate analyses of adults and juveniles. This is because chiffchaffs are notoriously difficult to age in autumn and winter, and the increased precision gained by taking this variable into account would be counter-balanced by reduced degrees of freedom and in an increased number of errors resulting from misclassifications. Age differences in wing-length are small (<2 mm) when compared to sex differences (ca. 6 mm; P. Catry and M. Lecoq, unpubl. data).

Although there are very minor differences in the wing-length distribution of male and female common and Iberian chiffchaffs (Ticehurst 1938, Svensson 2001), it is still possible to detect the bimodality caused by sexual size dimorphism, and estimate sex-ratios, in samples where the two species are pooled. Generally, there was a very good fit of the mixture models to the observed data (see Results). Some small, but significant, deviations were observed in the Senegal data set (Table 1). This was to be expected, given the very large sample sizes and the impossibility of a perfect match between models and field data. Possible reasons for an imperfect match are variations on wing-length with age and the fact that two different semispecies were almost certainly present in Senegal. However, the examination of histograms in Figs. 1 and 2 clearly support the results from the analyses, as the patterns are clear and well defined. It should be noted that the analyses performed did not aim

Table 1. Estimated chiffchaff *Phylloscopus [collybita]* sex composition of populations wintering in different geographical areas.

Study site/region	Latitude N (degrees)	% males \pm SE	Sample size	Fit of mixture model
Europe and N. Africa (<i>P. collybita</i>)				
England	50	83.2 \pm 5.3	85	$\chi^2_6 = 7.2$, P = 0.30
France	45	69.5 \pm 4.7	156	$\chi^2_6 = 1.5$, P = 0.96
N. Portugal	40.5	53.7 \pm 4.5	262	$\chi^2_8 = 8.9$, P = 0.35
C. Portugal	39	32.7 \pm 3.0	311	$\chi^2_8 = 4.9$, P = 0.77
SE Portugal	37	39.2 \pm 3.8	200	$\chi^2_8 = 7.6$, P = 0.48
SW Portugal	37	21.6 \pm 3.5	157	$\chi^2_6 = 8.1$, P = 0.23
Morocco	35	14.7 \pm 6.3	65	$\chi^2_3 = 3.6$, P = 0.61
Sub-Saharan Africa (<i>P. collybita</i> + <i>P. ibericus</i>)				
Mauritania	18	28.7 \pm 4.0	105	$\chi^2_3 = 3.8$, P = 0.58
N. Senegal	16.5	48.8 \pm 1.3	2,608	$\chi^2_{12} = 37.6$, P < 0.001
Gambia	13	30.0 \pm 4.0	161	$\chi^2_8 = 13.4$, P = 0.10

Fig. 1. Distribution of wing-lengths in common chiffchaff *Phylloscopus [collybita] collybita* samples caught in several regions of Europe and Africa. Note the general pattern of bimodality in the frequency distributions, with a predominance of long-winged birds (males) in the north, and short-winged birds (females) in the south.



to sex individual birds, just estimate the proportion of each sex in a sample. Therefore, the results cannot be affected by the disproportionate influence of a few wrongly sexed birds, as might be the case in an individually based analysis.

A small proportion of the birds caught in the United Kingdom in winter appeared to belong to the Scandinavian common chiffchaff subspecies *P. c. abietinus* that winters mostly in the eastern Mediterranean and East Africa (Cramp 1992), the presence of a few such birds in the UK sample should not affect our analyses in any meaningful way, given their similar body size to *P. c. collybita*.

Estimates of means and proportions are presented with associated standard errors. Data on sex-ratios (presented as the proportion of males in samples) were arc-sine transformed before statistical testing.

Results

Considering the chiffchaff superspecies, *Phylloscopus [collybita]*, we found no correlation between the proportion of males in samples taken in Europe and Africa and the latitude at which those samples were obtained ($r^2 = 0.25$, $N = 10$, $P = 0.14$; Table 1). However, when we

Djoudj

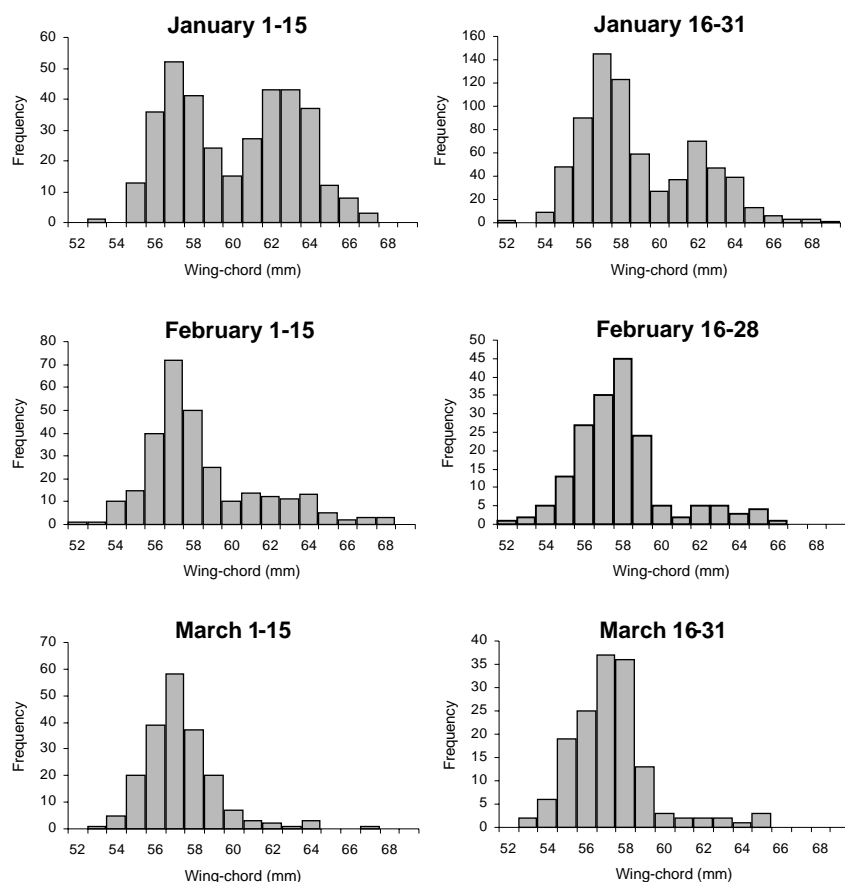


Fig. 2. Distribution of wing-lengths in chiffchaff *Phylloscopus [collybita]* samples caught in several periods in the Djoudj National Park (northern Senegal). Note the general pattern of bimodality in the frequency distributions, with a progressive reduction in the proportion of long-winged individuals (males).

restrict the analysis to locations north of the Sahara (excluding by this process most or all of the Iberian chiffchaffs from the data), the proportion of males in (common) chiffchaff samples becomes strongly and highly significantly positively correlated with latitude ($r^2=0.94$, $N=7$, $P<0.001$, see also Fig. 1).

The large numbers of chiffchaffs caught at the Djoudj, Senegal, during winter and early spring, allowed us to investigate if male chiffchaffs depart earlier than females from the wintering grounds. This hypothesis of differential timing of migration is clearly supported by the data (Fig. 2), as the proportion of males in chiffchaff samples declines steadily and sharply from early January to late March ($r^2=0.88$, $N=6$, $P=0.006$).

Discussion

In a recent revision, Cristol and colleagues (1999), managed to find robust published evidence for latitudinal segregation by sex in only 18 passerine species. Our study provides the first unequivocal evidence of differ-

ential migration distance in Old World warblers. Female common chiffchaffs migrate further than males, a pattern similar to all known passerine differential migrants.

Habitat segregation by sex could confound our results if there was some latitudinal trend in the habitats sampled. However, our data were collected from birds wintering in multiple habitats at most latitudes, and no obvious trends were detected (see brief habitat descriptions in the Methods section). Little is known about habitat segregation in chiffchaffs, although common chiffchaffs ringed at UK sites during autumn migration show even sex-ratios, irrespective of habitat (Reynolds 1978, Geen 1988). In central and southern Portugal, female-biased sex ratios can be found in a range of habitats, from wetland margins to scrub and orchards (own unpubl. data). Therefore, we find it unlikely that sex-specific habitat selection could have influenced the results of this study in a significant way.

In many passerines, males arrive ahead of females at stopover sites and to the breeding grounds (Izhaki and Maitav 1998, Kissner et al. 2003). Our study shows that

male chiffchaffs depart much earlier than females from African wintering grounds. Hence, departure time, and not (only) differential migration speed, is the cause for early male arrival (Marra et al. 1998, and Stouffer and Dwyer 2003 for similar conclusions concerning two North American migrants). On the other hand, male common chiffchaffs start autumn migration later than females (Geen 1988), thus spending an overall longer period on the breeding quarters.

The contrasting patterns of sexual segregation of chiffchaffs found north and south of the Sahara, and particularly the high proportion of males found in the important Senegalese wintering grounds, suggest (without proving) that there is a high proportion of Iberian chiffchaffs among the chiffchaffs wintering in West Africa, which is in agreement with recent suggestions that Iberian chiffchaffs are mostly, if not exclusively, trans-Saharan migrants (Svensson 2001, Pérez-Tris et al. 2003). We should also point out that, the typical Iberian chiffchaff call and song are never heard during winter in Portugal, and we know of no recoveries indicating that some birds are resident, further supporting the hypotheses that Iberian chiffchaffs are (long-distance) migrants.

Given that the chiffchaff is a strongly dimorphic species with larger males, the pattern of sexual segregation in the winter quarters described here supports both the body-size (or cold tolerance) hypothesis as well as the dominance hypothesis (because it seems most likely that the much larger males can easily establish dominance over females; e.g. Piper 1997). Considering that in most migratory passerines, including the chiffchaff, males are the territory defenders and that they generally arrive ahead of females to the breeding territories (Cramp 1992), the arrival-time hypothesis is also supported by the current data. However, our data do show that there is at least one other mechanism (early departure from wintering grounds) by which the sex more pressed to arrive early to the breeding grounds (generally assumed to be the males) can advance their arrival dates.

As pointed out by Cristol and colleagues (1999), when discussing differential migration, the problem in hand seems to be too intricate to be solved by testing single-factor hypotheses. The three hypotheses discussed here are not mutually exclusive, and often make similar predictions. However, comparisons of closely related species, such as the Iberian chiffchaff and the common chiffchaff, will ultimately prove to be essential for the resolution of this problem. Such comparisons will help identifying the key factors to be incorporated into optimality models that can predict relative distance of migration of different sex or age classes (Cristol et al. 1999). The chiffchaff superspecies might be a particularly suited model for such study, given the extreme morphological and ecological similarity between Iberian

and common chiffchaffs. However, to further research the migratory systems of these birds, new techniques will probably be needed, such as the tracking of migrants using stable isotopes and genetic markers (Rubenstein and Hobson 2004).

Acknowledgements – J.M.B. King is deceased; John Hutchinson and particularly Cyril Matthews facilitated access to the Gambia data files. Gonçalo Elias kindly supplied data on chiffchaffs ringed in central Portugal. We also thank all the volunteer ringers who helped with fieldwork in the Gambia, Senegal, Mauritania, Portugal, France and the U.K. Guy Jarry and Olivier Dehorter kindly made French chiffchaff data available from the Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO) Ringing Scheme. Vitor Encarnação allowed us access to the Portuguese ICN Ringing Scheme database. We thank the support of the Minister for Agriculture and Natural Resources for Gambia, and of the Senegal National Park Service. José Pedro Granadeiro introduced us to mixture programs. Stuart Bearhop, Roland Sandberg and two anonymous referees helped improving earlier drafts. Part of this study was supported by Fundação para a Ciência e a Tecnologia (FCT-Portugal) through the Programa plurianual (UlandD 331/94) and P. Catry benefited from a postdoctoral fellowship from FCT (Praxis XXI BPD/16304/98 and BPD/11631/02).

References

- Berthold, P. and Pulido, F. 1994. Heritability of migratory activity in a natural bird population. – *Proc. R. Soc. Lond. B* 257: 311–315.
- Catry, P., Catry, I., Catry, T. and Martins, T. 2003. Within and between winter-site fidelity in chiffchaffs *Phylloscopus collybita*. – *Ardea* 91: 213–220.
- Catry, P., Phillips, R. and Croxall, J. P. 2005. Sexual segregation in birds: patterns, processes and implications for conservation. – In: Ruckstuhl, K. E. and Neuhaus, P. (eds). *Sexual segregation in vertebrates*. Cambridge University Press, Cambridge.
- Nolan, V. Jr., ed. 1992. *The birds of the western Palearctic*, vol. VI. – Oxford University Press, Oxford.
- Cristol, D. A., Baker, M. B. and Carbone, C. 1999. Differential migration revisited. Latitudinal segregation by age and sex class. – In: Nolan, V. Jr., Ketterson, E. D. and Thompson, C. F. (eds) *Current Ornithol.* 15. Kluwer Academic/Plenum Publishers, New York.
- Gauthreaux, S. A. Jr. 1982. The ecology and evolution of avian migration systems. – In: *Avian Biology*. Vol. 6. – Academic Press, New York.
- Geen, G. R. 1988. The autumn migration of chiffchaffs at an inland site in south-east England. – *Ring. Migr.* 9: 65–67.
- Helbig, A. J., Knox, A. G., Parkin, D. T., Sangster, G. and Collinson, M. 2002. Guidelines for assigning species rank. – *Ibis* 144: 518–525.
- Hjort, C., Pettersson, J., Lindström, Å. and King, J. M. B. 1996. Fuel deposition and potential flight ranges of blackcaps *Sylvia atricapilla* and whitethroats *Sylvia communis* on spring migration in The Gambia. – *Ornis Svecica* 6: 137–144.
- Izhaki, I. and Maitav, A. 1998. Blackcaps *Sylvia atricapilla* stopping over at the desert edge; inter- and intra-sexual differences in spring and autumn migration. – *Ibis* 140: 234–243.
- Ketterson, E. D. and Nolan, V. Jr. 1976. Geographic variation and its climatic correlates in the sex-ratio of eastern-wintering dark-eyed juncos (*Junco hyemalis hyemalis*). – *Ecology* 57: 679–693.

- Ketterson, E. D. and Nolan, V. Jr. 1983. The evolution of differential bird migration. – In: Johnston, R. F. (ed.). *Curr. Ornithology*. Vol. I. Plenum Press, New York.
- Kissner, K. J., Waetherhead, P. J. and Francis, C. M. 2003. Sexual size dimorphism and timing of spring migration in birds. – *J. Evol. Biol.* 16: 154–162.
- Knox, A. G., Collinson, M., Helbig, A. J., Parkin, D. T. and Sangster, G. 2002. Taxonomic recommendations for British birds. – *Ibis* 144: 707–710.
- Lecoq, M. and Catry, P. 2003. Diurnal tape-luring of wintering chiffchaffs results in samples with biased sex ratios. – *J. Field Ornithol.* 74: 230–232.
- Marra, P. P., Hobson, K. A. and Holmes, R. T. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. – *Science* 282: 1884–1886.
- MacDonald, P. D. M. and Pitcher, T. J. 1979. Age-groups from size-frequency data: a versatile and efficient method of analysing distribution mixtures. – *J. Fish. Res. Board of Canada* 36: 987–1001.
- Myers, J. P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. – *Can. J. Zool.* 59: 1527–1534.
- Pérez-Tris, J., Ramírez, Á. and Tellería, J. L. 2003. Are Iberian chiffchaffs *Phylloscopus (collybita) brehmii* long-distance migrants? An analysis of flight-related morphology. – *Bird Study* 50: 146–152.
- Piper, W. H. 1997. Social dominance in birds: early finding and new horizons. – In: Nolan V., Jr., Ketterson, E. D. and Thompson C. F. (eds) *Current Ornithol.* 14. Plenum Press, New York, pp. 125–187.
- Reynolds, A. 1978. Chiffchaffs at Rye Meads. – *Ring. Migr.* 2: 38–41.
- Rodenhouse, N. L., Sherry, T. W. and Holmes, R. T. 1997. Site-dependent regulation of population size: a new synthesis. – *Ecology* 78: 2025–2042.
- Rubenstein, D. R. and Hobson, K. A. 2004. From birds to butterflies: animal movement patterns and stable isotopes. – *Trends Ecol. Evol.* 19: 256–263.
- Salomon, M., Voisin, J.-F. and Bried, J. 2003. On the taxonomic status and denomination of the Iberian chiffchaffs. – *Ibis* 145: 87–97.
- Sauvage, A., Rumsey, S. and Rodwell, S. 1998. Recurrence of Palaearctic birds in the lower Senegal river valley. – *Malimbus* 20: 33–53.
- Sherry, T. W. and Holmes, R. T. 1996. Winter habitat quality, population limitation and conservation of Neotropical-Nearctic migrant birds. – *Ecology* 77: 36–48.
- Stouffer, P. C. and Dwyer, G. M. 2003. Sex-biased winter distribution and timing of migration of hermit thrushes (*Catharus guttatus*) in eastern North America. – *Auk* 120: 836–847.
- Svensson, L. 2001. The correct name of the Iberian chiffchaff *Phylloscopus ibericus* Ticehurst 1937, its identification and new evidence of its winter grounds. – *Bull. Brit. Ornithol. Club* 121: 281–296.
- Terril, S. B. and Berthold, P. 1989. Experimental evidence of endogenously programmed differential migration in the blackcap (*Sylvia atricapilla*). – *Experientia* 45: 207–209.
- Ticehurst, C. B. 1938. A systematic review of the Genus *Phylloscopus*. – *Brit. Mus.*, London.
- Zink, G. 1973. *Der Zug europäischer Sinvögel. Ein Atlas der Wiederfunde beringter Vögel.* – *Vogelwarte Radolfzell, Möggingen.*

(Received 16 April 2004, revised 24 January 2005, accepted 17 February 2005.)