

RESEARCH LETTERS

Research letters are short papers (≤ 5 printed pages, about 4000 words), ideally presenting new and exciting results. Letters will be given priority, whenever possible, in the publication queue. Contributions should be as concise as possible. An abstract is required.

JOURNAL OF AVIAN BIOLOGY 36: 6–11, 2005

Non-random distribution of ring recoveries from trans-Saharan migrants indicates species-specific stopover areas

Thord Fransson, Sven Jakobsson and Cecilia Kullberg

Fransson, T., Jakobsson, S. and Kullberg, C. 2005. Non-random distribution of ring recoveries from trans-Saharan migrants indicates species-specific stopover areas. – J. Avian Biol. 36: 6–11.

Many long-distance migrant birds regularly have to pass ecological barriers, like the Saharan desert, where fuelling is very difficult, and large fuel loads have to be stored in advance. In this paper, we have investigated how seven species of birds are distributed in autumn close to the Saharan desert in the eastern Mediterranean area by using ring recoveries from northern Europe. The result clearly shows that the species included are not randomly distributed at this point, about 3,000 km from the breeding area. Birds from rather large breeding areas were shown to converge in confined areas, which in several cases completely differ between species. This means that birds of the same species have to follow different migratory directions depending on the location of their starting point. The observed pattern support earlier findings indicating that birds, in combination with a clock-and-compass orientation procedure, must use some external cues in order to find confined species-specific areas. The possibility for birds to use information from the Earth's magnetic field as an external cue in this area is discussed.

T. Fransson (correspondence), Swedish Museum of Natural History, Bird Ringing Centre, Box 50 007, SE-104 05 Stockholm, Sweden. E-mail: thord.fransson@nrm.se. S. Jakobsson and C. Kullberg, Department of Zoology, Stockholm University, SE-106 91 Stockholm, Sweden.

Many bird species accomplish bi-annual migratory movements in order to exploit seasonally available resources. (Alerstam and Lindström 1990, Berthold 1996). Both distances and time involved in these movements varies considerably. Some species can be on migration for as much as six months of the year, and travel about 20,000 km. Passerine birds have been shown to use both celestial cues and information from the Earth's magnetic field to choose and maintain a species- or population-specific migratory direction (Able 1993, Wiltchko and Wiltchko 1995). Fat is the main fuel for migratory flights, but large fuel loads entails increased flight costs as well as reduced escape performance at a predator attack (Blem 1980, Alerstam and Lindström 1990, Kullberg et al. 1996, Kullberg et al. 2000). Most

bird species therefore seem to accumulate rather small fat deposits (20–30% of lean body mass), and refuel at several successive stopover sites (Alerstam and Lindström 1990). However, many long-distance migratory birds have to face the challenge of passing vast ecological barriers, where fuelling is not possible and very large fuel loads have to be stored in advance. The passage of the Saharan desert involves flight distances of at least 1500 km with hardly any refuelling possibilities (Moreau 1961, Biebach 1990). In spite of this, passerine birds regularly pass the desert and as many as 3–5 billion has been estimated to be involved (Moreau 1972). Birds have been found to double their mass (100% increase of lean body mass) by means of fat storage prior to this barrier (Fry et al. 1970).

In a study by Thorup and Rabøl (2001), three long distance migratory species show a higher directional concentration than expected from a simple clock-and-compass model ('vector orientation'). The authors conclude that in addition, some external cues must be involved in guiding a naïve bird to a species-specific wintering area. In accordance, we have in recent studies shown that birds might use information from the Earth's magnetic field as an external cue to decide where to accumulate the extensive fuel loads necessary for successful trans-Saharan flights (Fransson et al. 2001, Kullberg et al. 2003). Furthermore, ring recoveries of thrush nightingales *Luscinia luscinia* from northern Europe were found to be highly concentrated to a restricted area in northern Egypt (Kullberg et al. 2003). If confined species-specific stop over areas are a general pattern in long-distance migrants prior to the trans-Saharan crossing remains to be investigated. In this study ring recoveries from northern Europe have been used to investigate how seven migratory species are distributed in the eastern part of the Mediterranean area during autumn migration.

Material and methods

Only ten species of passerines breeding in northern Europe pass the eastern part of the Mediterranean area on their way to their wintering grounds in sub-Saharan Africa (Cramp 1988, 1992, Cramp and Perrins 1993, 1994). Due to low numbers of ring recoveries (less than 5) in three species (river warbler *Locustella fluviatilis*, marsh warbler *Acrocephalus palustris* and collared flycatcher *Ficedula albicollis*), we have restricted our analysis to seven species; thrush nightingale, barred warbler *Sylvia nisoria*, lesser whitethroat *Sylvia curruca*, common whitethroat *Sylvia communis*, blackcap *Sylvia atricapilla*, willow warbler *Phylloscopus trochilus* and red-backed shrike *Lanius collurio*. Of these, the thrush nightingale, the barred warbler, the lesser whitethroat and the red-backed shrike are almost exclusively found in this area, while on passage from breeding sites in Europe to wintering areas in sub-Saharan Africa, while the other species have populations breeding in Europe passing the western part of the Mediterranean area as well (Cramp 1988, 1992, Cramp and Perrins 1993). The study area we defined (Fig. 1) covers most of the passage of birds from Europe along the eastern flyway, and the area in Libya to the west holds very few recoveries (Zink 1973, 1975). We obtained ring recoveries from birds ringed in Denmark (the Zoological Museum in Copenhagen), Sweden (the Swedish Museum of Natural History), Norway (Stavanger Museum) and Finland (the Finnish Museum of Natural History). Ringing started in those countries during the beginning of the last century, but most of the recoveries included are from the last 40

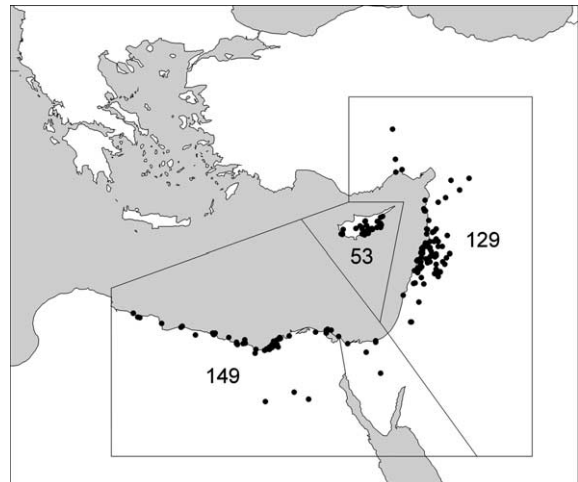


Fig. 1. The study area in the eastern part of the Mediterranean and all the recoveries included from birds ringed in Denmark, Norway, Sweden, Finland and at the Biological Station Rybachy, Kaliningrad (n = 331). The division of the area into smaller parts is also shown as well as the total number of recoveries within the different areas.

years, which coincides with an overall increase in the number of passerine birds ringed in northern Europe. We have also included published recoveries from the Biological Station Rybachy on the Courish Spit, Kaliningrad, from the period 1956–1997, found in the study area (Bolshakov et al. 2001). Recoveries used in the analysis are from the autumn migration, and we have included all recoveries that are reported between July and December. The total number of autumn recoveries is 331. The largest number of recoveries refers to adult birds (63%), being experienced migrants, while a smaller proportion consists of juvenile birds (26%) on their first migration. A small part of the material (10%) refers to recoveries of birds with unknown ringing age found in the same autumn as they were ringed, most of them probably on their first migration. Based on geography and the distribution of recoveries, we have divided the study area into three parts in order to test whether the recoveries from the different species are randomly distributed or not (Fig. 1). Parts of Libya and Egypt are included in one area, Cyprus in another and the third area include Israel, Jordan, Lebanon, Syria and parts of Turkey. Traditional hunting of migratory birds has occurred in this area for a long time (Moreau and Dolp 1970, Woldhek 1979), and most of the recoveries are from birds killed.

Results

Ring recoveries from the seven species were not randomly distributed between the three areas (Pearson χ^2 : $\chi^2 = 254.3$, $df = 12$, $P < 0.001$; Table 1). Red-backed shrike, thrush nightingale and common whitethroat are

Table 1. Number of ring recoveries of the seven species from the different areas.

Species	Libya and Egypt	Cyprus	Israel, Jordan, Lebanon, Syria and Turkey	Total
Thrush nightingale	19	0	0	19
Barred warbler	0	0	14	14
Lesser whitethroat	13	21	68	102
Common whitethroat	20	0	2	22
Blackcap	0	28	34	62
Willow warbler	64	4	10	78
Red-backed shrike	33	0	1	34
Total	149	53	129	331

more or less exclusively found in one area, northern Egypt (Table 1; Fig. 2a–c), while the barred warbler is only found in another area, Turkey, Syria and Lebanon (Table 1; Fig. 2d). There is not a single ring recovery of blackcaps in northern Egypt while they are equally common in the two other areas (Table 1; Fig. 2e). The two last species, lesser whitethroat and willow warbler, are found in all three areas, but the main area differs (Table 1; Fig. 2f–g). The majority of willow warblers is reported from northern Egypt while lesser whitethroats are more commonly found in Syria, Lebanon and Israel. It is clear that several species start off from a relatively larger breeding area and that they converge in a much smaller area in front of the Saharan desert. This is especially evident in the thrush nightingale (Fig. 2a), the barred warbler (Fig. 2d) and the blackcap (Fig. 2e).

Discussion

Our result shows that the species under study are not evenly distributed in the eastern Mediterranean area. This strongly suggests that many long-distance migrants use species-specific stopover areas in front of the Saharan desert. The non-random pattern of ring recoveries observed cannot be explained by variation of hunting effort in the different areas, since hunting for small birds takes place in large parts of the Mediterranean and especially so in the included three areas. A variety of hunting methods is used in the Mediterranean, and they are known to differ between the three areas. In northern Egypt the main method used is covering trees with nets and in Cyprus, Lebanon and Syria lime-sticks are commonly used (Moreau and Dolp 1970, Woldhek 1979). However, since the methods used are not species-specific, and all the species included are small sized birds that use more or less similar habitats during migration, we have no reason to believe that the observed differences in distribution have been caused by differences in hunting methods.

The species included in this study have larger longitudinal variation in their breeding areas than at the Mediterranean passage. This means that individuals of the same species have to use different migratory directions depending on the location of their starting

point (breeding area). Recoveries show that lesser white-throats and red-backed shrikes from Western Europe also pass this area in the eastern Mediterranean (Zink 1973, 1975, Biebach et al. 1983, Wernham et al. 2002), resulting in an even larger within-species variation in migratory directions. Thorup and Rabøl (2001) found that some species of long-distance migrants are widely distributed in the Mediterranean and that they concentrate further south when approaching the wintering area. However, several of the species included in our study show a pattern where they already are concentrated within a confined area when they pass the Mediterranean. A challenging evolutionary question is how this regional stopover specificity has evolved. It is reasonable to believe that the post-glacial recolonization from south-eastern refuges is involved (cf. Hewitt 2000, Kvist et al. 2004). The observed differences in distribution between the included species in our study might have been fine-tuned as a result of species-specific habitat requirements. It is interesting to note that both the willow warbler and the lesser whitethroat, which have relatively broad foraging repertoire, have a more widespread distribution than the other species.

Since extensive fuel loads are of decisive importance for a successful trans-Saharan flight, it is reasonable to believe that strong selection has acted on birds in order to find well-defined species/population specific stopover sites that enable the necessary preparation before the barrier. That fine-tuned fuelling strategies exist in connection with the trans-Saharan passage have been demonstrated by Rubolini et al. (2002), showing that the distance to be covered across the Saharan desert affects the pre-migratory fuel stores in barn swallows *Hirundo rustica*. It has recently been suggested that migratory birds do not show the same site philopatry to stopover sites as often observed concerning breeding and winter sites (Catry et al. 2004). There are few detailed stopover studies close to the barrier crossing, and we would not be surprised if faithfulness to such stopover sites is a more common pattern. It is interesting to note that a relatively high recapture rate between seasons was found in migrants in southern Tunis, at the desert edge, in spring (Moreau 1961).

The specific and concentrated distribution of ring recoveries in this study, at a distance of about 3000 km

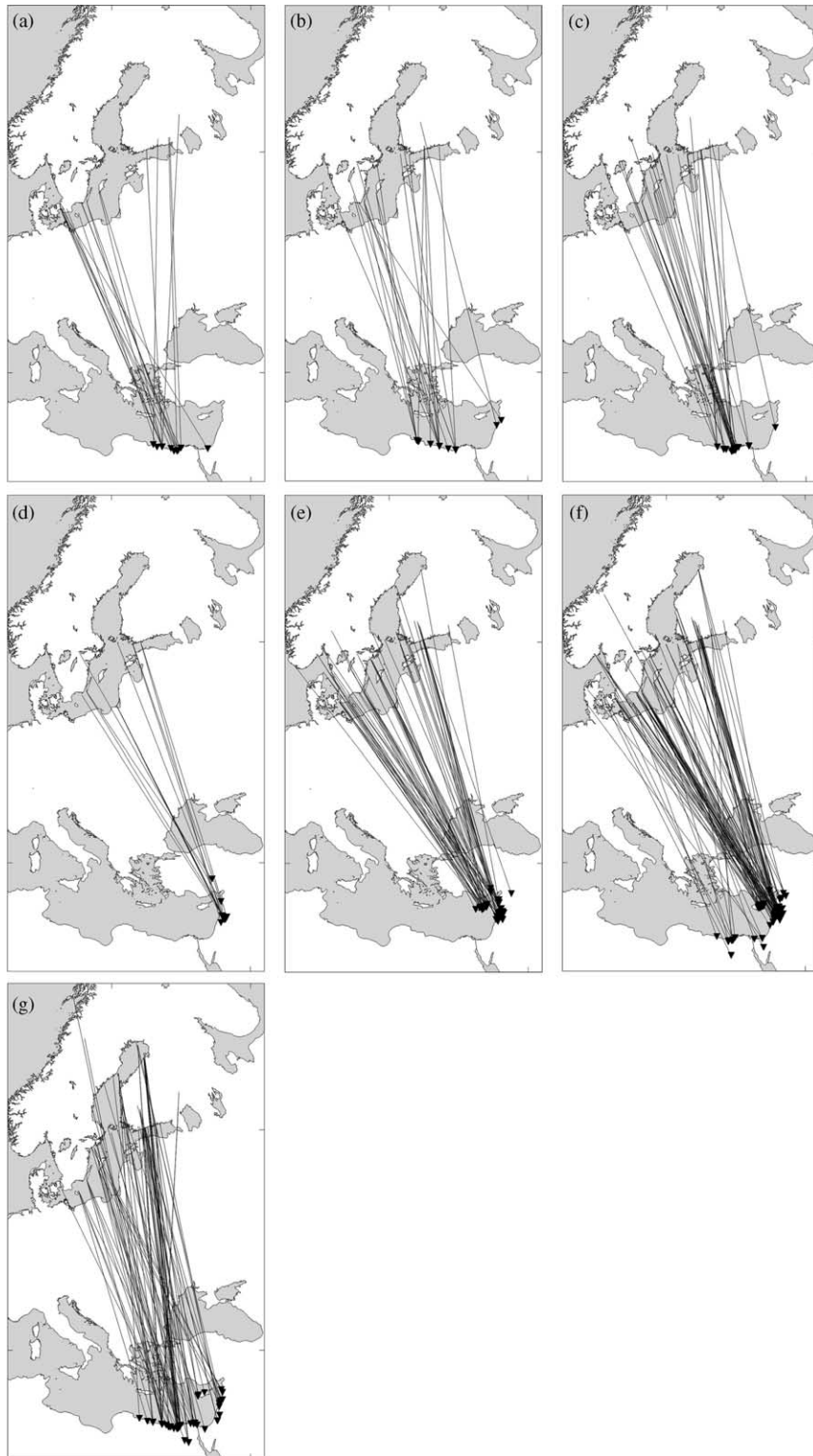


Fig. 2. Recoveries of birds ringed in Denmark, Norway, Sweden, Finland and at the Biological Station Rybachy, Kaliningrad, and found in the study area in the eastern Mediterranean. Lines connect the ringing site with the recovery site. (a) thrush nightingale, (b) common whitethroat, (c) red-backed shrike, (d) barred warbler, (e) blackcap, (f) lesser whitethroat and (g) willow warbler.

from the breeding area, indicates that birds use external cues for finding their species-specific stopover areas, which also has been suggested by Thorup and Rabøl (2001) concerning birds ability to find their wintering area. One such important cue may be magnetic information (Beck and Wiltschko 1988, Fransson et al. 2001, Fischer et al. 2003, Kullberg et al. 2003). A prerequisite for birds to use geomagnetic information as a cue to locate a small area is the ability to detect small changes in the magnetic field. The bobolink *Dolichonyx oryzivorus*, a long-distance migrant, has been shown to detect changes of 200 nT electrophysiologically (Semm and Beason 1990), and field studies on pigeons, sharks, whales (reviewed in Walker et al. 2002) and lobsters (based on calculations from data in Boles and Lohmann 2003), reports on sensitivities as small as between 10 and 50nT. A recent study on white-crowned sparrows *Zonotrichia leucophrys gambelii* also indicate that the magnetoreceptors in birds are extremely sensitive to small changes (less than 3°) in the angle of the geomagnetic inclination (Åkesson et al. 2001). Differences in the total intensity and inclination of the magnetic field between the centres of the three areas in this study are within the range of these estimates (Libya and Egypt (31°00'N 29°00'E): 43 186 nT, 45.2°; Cyprus (35°00'N 33°45'E): 45 234 nT, 51.5°; Israel, Jordan, Syria and parts of Turkey (34°00'N 36°30'E): 45 138 nT, 50.4°), indicating that geomagnetic cues can be a relevant external cue for these species to find their species-specific stopover areas before the trans-Saharan passage.

The pattern described in this study could have implications for nature protection. The passage of the Saharan desert is critical for many migratory birds and of utmost importance for the diversity of breeding birds in northern Europe. There are studies showing that several long-distance migratory species breeding in northern Europe have decreased in numbers during the last 15 years (Karlsson et al. 2002, Lindström and Svensson 2004), but the reasons for these declines are not known. If there exist well-defined species-specific stopover areas important for extensive fuelling these localities are likely to function as key areas (maybe as important as wetlands are for many migratory waterbirds) for preserving long-distance migratory species.

Acknowledgements – The bird ringing centres at the Zoological Museum in Copenhagen, the Swedish Museum of Natural History in Stockholm, Stavanger Museum in Norway and the Finnish Museum of Natural History in Helsinki kindly let us use their data on ring recoveries. We thank Kasper Thorup for valuable comments on the manuscript. CK is funded by the Swedish Research Council.

References

Able, K. P. 1993. Orientation cues by migratory birds: a review of cue-conflict experiments. – *Trends Ecol. Evol.* 8: 367–371.

- Alerstam, T. and Lindström, Å. 1990. Optimal bird migration: the relative importance of time, energy, and safety. – In: Gwinner, E. (ed.). *Bird migration: the physiology and ecophysiology*. Springer-Verlag, Berlin, pp. 331–350.
- Åkesson, S., Morin, J., Muheim, R. and Ottosson, U. 2001. Avian orientation at steep angles of inclination: experiments with migratory white-crowned sparrows at the magnetic North Pole. – *Proc. R. Soc. Lond. B* 268: 1907–1913.
- Beck, W. and Wiltschko, W. 1988. Magnetic factors control the migratory direction of pied flycatchers (*Ficedula hypoleuca Pallas*). – In: Ouellet, H. (ed.). *Acta XIX Congr., Intern. Ornithol.*, pp. 1955–1962.
- Berthold, P. 1996. *Control of bird migration*. – Chapman & Hall, London.
- Biebach, H. 1990. Strategies of Trans-Saharan Migrants. – In: Gwinner, E. (ed.). *Bird Migration*. Berlin Heidelberg, pp. 352–367.
- Biebach, H., Dallmann, M., Schuy, W. and Siebenrock, K.-H. 1983. Die Herbstzugrichtung von Neuntöttern (*Lanius collurio*) auf Karpathos (Griechenland). – *J. Ornithol.* 124: 251–257.
- Blem, C. R. 1980. The energetics of migration. – In: Gautreaux Jr., S. A. (ed.). *Animal migration, Orientation and Navigation*. Academic Press, Toronto, pp. 125–218.
- Boles, L. C. and Lohmann, K. J. 2003. True navigation and magnetic maps in spiny lobsters. – *Nature* 421: 60–63.
- Bolshakov, C. V., Shapoval, A. P. and Zelenova, N. P. 2001. Results of ringing by the Biological Station “Rybachy” on the Courish Spit: long-distance recoveries of birds ringed in 1956–1997. Part 1. – *Avian Ecol. Behav. Suppl.* 1: 1–126.
- Catry, P., Encarnacao, V., Araújo, A., Fearon, P., Fearon, A., Armelin, M. and Delaloye, P. 2004. Are long-distance migrant passerines faithful to their stopover sites? – *J. Avian Biol.* 35: 170–181.
- Cramp, S. 1988. *The birds of the Western Palearctic*. Vol V. – Oxford University Press, Oxford.
- Cramp, S. 1992. *The birds of the Western Palearctic*. Vol VI. – Oxford University Press, Oxford.
- Cramp, S. and Perrins, C. M. 1993. *The birds of the Western Palearctic*. Vol VII. – Oxford University Press, Oxford.
- Cramp, S. and Perrins, C. M. 1994. *The birds of the Western Palearctic*. Vol VIII and IX. – Oxford University Press, Oxford.
- Fischer, J. H., Munro, U. and Phillips, J. B. 2003. Magnetic navigation by an avian migrant? – In: Berthold, P., Gwinner, E. and Sonnenschein, E. (eds). *Avian migration*. Springer-Verlag, Heidelberg New York, pp. 141–154.
- Fransson, T., Jakobsson, S., Johansson, P., Kullberg, C., Lind, J. and Vallin, A. 2001. Bird migration: magnetic cues trigger extensive refuelling. – *Nature* 414: 35–36.
- Fry, C. H., Ash, J. S. and Ferguson-Lees, I. J. 1970. Spring weights of some Palearctic migrants at Lake Chad. – *Ibis* 112: 58–82.
- Hewitt, G. 2000. The genetic legacy of the Quaternary ice ages. – *Nature* 405: 907–913.
- Karlsson, L., Ehnbohm, S., Persson, K. and Walinder, G. 2002. Changes in numbers of migration species at Falsterbo, South Sweden during 1980–1999, as reflected by ringing totals. – *Ornis Svecica* 12: 113–137.
- Kullberg, C., Fransson, T. and Jakobsson, S. 1996. Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*). – *Proc. R. Soc. Lond. B* 263: 1671–1675.
- Kullberg, C., Jakobsson, S. and Fransson, T. 2000. High migratory fuel loads impair predator evasion in sedge warblers. – *Auk* 117: 1034–1038.
- Kullberg, C., Lind, J., Fransson, T., Jakobsson, S. and Vallin, A. 2003. Magnetic cues and time of season affect fuel deposition in migratory thrush nightingales (*Luscinia luscinia*). – *Proc. R. Soc. Lond. B* 270: 373–378.
- Kvist, L., Viiri, K., Dias, P. C., Rytkönen, S. and Orell, M. 2004. Glacial history and colonization of Europe by the blue tit *Parus caeruleus*. – *J. Avian Biol.* 35: 352–359.

- Lindström, Å. and Svensson, S. 2004. Monitoring population changes of birds in Sweden. Report. – Department of Ecology, Lund University. 68 pp.
- Moreau, R. E. 1961. Problems of Mediterranean-Saharan migration. – *Ibis* 103: 373–427, 580–623.
- Moreau, R. E. 1972. The Palearctic–African bird migration system. – Academic Press, London and New York.
- Moreau, R. E. and Dolp, R. M. 1970. Fat, water, weights and wing-lengths of autumn migrants in transit on the northwest coast of Egypt. – *Ibis* 112: 209–228.
- Rubolini, D., Pastor, A. G., Pilastro, A. and Spina, F. 2002. Ecological barriers shaping fuel stores in barn swallows *Hirundo rustica* following the central and western Mediterranean flyways. – *J. Avian Biol.* 33: 15–22.
- Semm, P. and Beason, R. 1990. Responses to small magnetic variations by trigeminal system of the bobolink. – *Brain Res. Bull.* 25: 735–740.
- Thorup, K. and Rabøl, J. 2001. The orientation system and migration pattern of long-distance migrants: conflict between model predictions and observed patterns. – *J. Avian Biol.* 32: 111–119.
- Walker, M. M., Dennis, T. E. and Kirschvink, J. L. 2002. The magnetic sense and its use in long-distance navigation by animals. – *Curr. Opin. Neurobiol.* 12: 735–744.
- Wernham, C., Toms, M., Marchant, J., Clarke, J., Siriwardena, G. and Baillie, S. (eds). 2002. The migration atlas: movements of the birds of Britain and Ireland. – T. & A. D. Poyser, London.
- Wiltschko, R. and Wiltschko, W. 1995. Magnetic orientation in animals. – Springer, Berlin.
- Woldhek, S. 1979. Bird killing in the Mediterranean. – European committee for the prevention of mass destruction of migratory birds. Zeist, The Netherlands, 62 pp.
- Zink, G. 1973. Der Zug Europäischer Singvögel. Ein Atlas der Wiederfunde beringter Vögel. 1. Lieferung. – Vogelwarte Radolfzell, Konstanz.
- Zink, G. 1975. Der Zug Europäischer Singvögel. Ein Atlas der Wiederfunde beringter Vögel. 2. Lieferung. – Vogelzug-Verlag, Möggingen.

(Received 4 June 2004, revised 13 September 2004, accepted 17 September 2004.)