

Migratory direction established in inexperienced bird migrants in the absence of magnetic field references in their pre-migratory period and during testing

J. RABØL¹ and K. THORUP²

¹ Biological Institute, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark (E-mail: jrabol@bi.ku.dk)

² Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark (E-mail: kthorup@snm.ku.dk)

Received 31 May 2005, accepted 1 March 2006

Several studies have investigated the importance of different orientational cues that pre-migratory, naïve bird migrants might use to develop their appropriate migratory orientation. We tested the hypothesis that, without any interplay with the magnetic compass in the pre-migratory period, celestial rotation alone cannot lead to any migratory orientation that differs significantly from due south, i.e. celestial rotation is used as a reference only and it is set by the geomagnetic compass to the species-specific migration direction. In the present study, juvenile whitethroats, *Sylvia communis*, trapped in the field soon after fledging, developed appropriate migratory orientation when held in outdoor cages in full view of celestial cues, but in a strong, heterogeneous magnetic field without any meaningful, magnetic directional information and tested in a strong and approximately vertical magnetic field. The migratory orientation of these birds did not differ from that of birds held in an undisturbed magnetic field, and both differed significantly from south. Thus, the birds established a deviation from south (away from celestial rotation) in the absence of meaningful magnetic information in the pre-migratory phase. This indicates that magnetic information is not necessary for establishing the appropriate migratory direction when natural celestial cues are available in the pre-migratory period.

KEY WORDS: migration direction, orientation, animal behaviour, whitethroat, *Sylvia communis*.

Introduction	44
Material and methods	44
Results	46
Discussion	47
Acknowledgements	50
References	50

INTRODUCTION

The development of the species-specific migratory direction in naïve bird migrants is important for our understanding of the migratory orientation system in birds. The primary role of celestial rotation in the development of migratory direction was demonstrated by EMLEN (1970). By manipulating the position of the stellar rotation point in a planetarium, it was shown how celestial rotation guided the orientation of young indigo buntings, *Passerina cyanea*, in their first autumn.

However, several studies indicate that the magnetic field is crucial in the development of the inherited migration direction. According to e.g. WEINDLER et al. (1996, 1997), WILTSCHKO et al. (1998) and WILTSCHKO & WILTSCHKO (1999, 2003) the magnetic field and compass together with celestial rotation play an important role for the development of a proper migration direction. Experiencing celestial rotation only, without magnetic interaction in the pre-migratory period, a first-time migrant will orient due south (away from celestial rotation) and not south-west as in the case of e.g. a German garden warbler, *Sylvia borin* (GWINNER & WILTSCHKO 1978). The experimental evidence for that finding is only a few tests carried out under a simple, stationary '16-star-sky'. It would be better if these results were confirmed through tests under a natural stellar sky. In the present study, such experiments are described in which first-time whitethroats, *Sylvia communis*, from their pre-migratory beginning well into their migratory season were caged and tested outdoors in a disturbed magnetic field, but with access to celestial cues both day and night.

MATERIAL AND METHODS

Twelve juvenile whitethroats (the experimentals) from a local breeding population were trapped in mist-nets on the island Endelave (55°N, 10°E), Denmark, on the 6-10 July, 2000, and immediately transferred to outdoor cages (plastic baskets) in pairs. From 11 July the birds were placed within disturbed magnetic fields (see below). Eleven other birds (the controls) were trapped on 12 July (4 individuals), 30 July (6) and 2 August (1). These, too, were placed in pairs in outdoor cages in the normal magnetic field shortly after being caught. All 23 birds were released on 11 September. The birds could observe their surroundings and the sky through the sides and the open mesh top of the baskets.

The experimentals were tested as juveniles in magnetic fields, presumably unfit for migratory orientation or interaction with the celestial rotation for the development of a proper standard orientation. As seen in Fig. 1, two wooden perches (north/south and east/west) were added to the baskets just below the covering mesh. The experimentals had two strong bar-magnets attached to the underside of the east/west perch, which produced a very strong and heterogeneous magnetic field within the cage. We chose bar-magnets (instead of coils) to allow a substantial number of birds to be kept as experimentals. Fig. 1 shows the (horizontal) directions of magnetic north at different positions within the cage when the magnetic norths of the two magnets pointed west. The birds spent most of their time on the perches (in particular during migratory activity). The magnetic field was chaotic in the mid and upper parts of the cages. Five centimetres above the perches at the approximate level of the birds' heads, the intensity was up to 50 times (Table 2) stronger than the normal geomagnetic field (ca 48 000 nT). The lowest intensity was found near the bottom of the cages (70 000 nT). Once a day (between midnight and early morning), the cages were rotated 180°, i.e. the bars' magnetic north was due east every other day and night, and the resulting bottom cage magnetic north was then directed about east-north-east. This extremely varying (heterogeneous in time and space) and strong magnetic field is very unlikely to provide a magnetic reference (WILT-

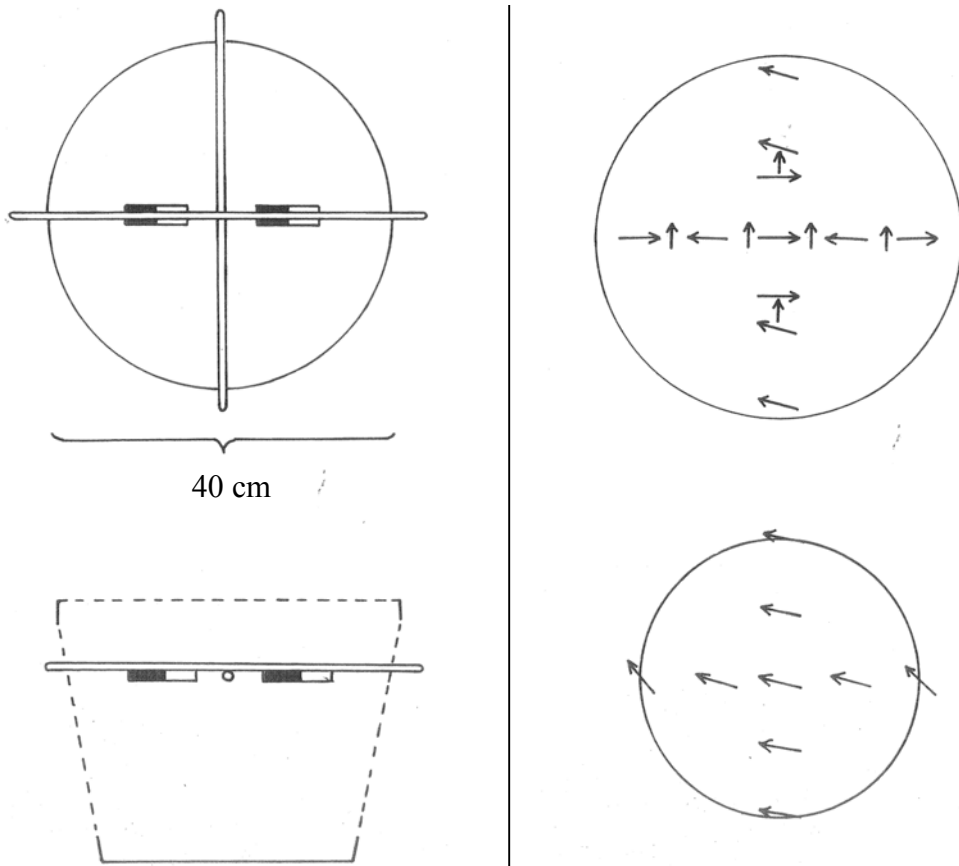


Fig. 1. — Left column: The cage from above (top) and from the side (below). The birds were caged in pairs. In the experimentals, two bar magnets were placed on the east/west oriented stick as depicted, creating a magnetic field shown in right column. Right column: Direction (magnetic north) of the horizontal component of the resulting magnetic field 5 cm above the sticks (top) and 5 cm above the bottom (below), when magnetic north of the bar magnets was pointing west. Geomagnetic north is pointing upward. See text and Table 2 for further details.

SCHKO & WILTSCHKO 1995) or useful information about the direction of the magnetic north of the geomagnetic field (W. WILTSCHKO in litt.).

When the experimentals were tested strong bar-magnets were placed in the spouts of the funnels. Magnetic south of these bar-magnets was placed a few centimetres below the pad at the bottom of the funnel, and the resultant magnetic field on the pad was very strong (50 times the normal geomagnetic field), heterogeneous and with an inclination at approx. + 90°, i.e. vertical.

The cages of the controls and the experimentals were placed on two different, 240 cm by 120 cm, tables in a forest glade. Their heights were about 1 m and they were adjusted to an absolute horizontal level. The funnel tests were also performed on these tables. In order to screen for any strong sun or rain the cages could be covered with a sheet of plywood (60 cm by 60 cm).

Between 25 August and 10 September experiments were carried out on 10 clear and starry nights. On any other night the sky was overcast and/or rainy. From sunset until at least one and a half hours after sunset the birds were in their cages before being tested for about one and a half hours in the funnels. Because of a late descending moon the last three experiments were carried out after midnight and lasted a little longer, about 2 hr.

The funnel activity was registered by means of the scraping patterns in typewriter correction papers mounted on the insides of the funnels. In the analyses, we used the estimated mean direction (for details of this method see RABØL 1970 and MOURITSEN & LARSEN 1998) or the major peak in case of a bimodal activity pattern with a major and a minor peak. When the birds displayed no activity, dis-orientation or bimodal orientation with two equally large peaks, no directional information was entered into the analyses of that individual bird night. Sample directional statistics follow STEPHENS (1972) and BATSCHLET (1981). Sample and grand mean vectors were calculated following e.g. HELBIG et al. (1989), WEINDLER et al. (1996) and WILTSCHKO et al. (2001) using all individual mean directions. The significance of the sample mean vectors are given according to the Rayleigh test ('*': $P < 0.05$, '***': $P < 0.01$, '****': $P < 0.001$).

Some controls were caught late in the season close to the start of migration. However, there was no significant difference between control birds that were caught early or late. The two grand mean vectors were 162° , 0.955^* ($N = 4$, early birds) and 147° , 0.831^* ($N = 6$, late birds). Omitting the most extreme, late bird (with a mean direction of 80°) changed the latter grand mean vector to 158° , 0.937^* .

We found no directional influence of the bar magnets. The orientation of the experimentals did not differ between nights when the magnetic north was turned west (154° , 0.585 , $N = 5$) or east (170° , 0.889^* , $N = 5$). The slight difference is in the direction to be expected as influenced by the magnetic compass. However, the control birds showed a similar difference (145° , 0.921^{**} ($N = 5$), and 161° , 0.917^{**} ($N = 5$)).

In their cages, the birds had ad libitum access to food (including mealworms), vitamins and water. The birds were caged outdoors from their capture between 6 July to 2 August (2000) until their release on 11 September (by the end of the normal migratory season for Danish whitethroats), all in good condition. As the directional behaviour of the experimentals did not differ from that of the controls (see results section) their release raised no ethical problems.

Permission to catch the birds was obtained from the Copenhagen Bird Ringing Centre, and permission to perform the experiments was obtained from the Wildlife Management Division, Danish Forest and Nature Agency, Ministry of Environment.

RESULTS

Table 1 gives information on each bird. Fig. 2 shows the individual mean directions and grand mean vectors. The grand mean vectors are 153° , 0.788^{***} ($N = 12$, experimentals), and 154° , 0.873^{***} ($N = 10$, controls). The 95% confidence intervals are $\pm 25^\circ$ and 23° , respectively, i.e. both mean directions deviate significantly from due south. There is no significant difference between the two mean directions, nor any significant difference between the two concentrations ($F_{11,9} = 1.63$, $P = 0.24$).

Considering the sample distributions of all individual directions (including the major peaks of bi-modal patterns) the following sample mean vectors were calculated: 156° , 0.504^{***} ($N = 63$, experimentals) and 156° , 0.610^{***} ($N = 66$, controls). Again, both mean directions deviate significantly from due south (the 95% confidence intervals are $\pm 22^\circ$ and 16° , respectively).

Table 1.

Individual mean vectors (Dir., Conc.), nightly mean directions and number of tests ('#') with unidirectional activity (including bimodal patterns with major peaks). Bimodal orientations with a major peak (e.g. 85°/(255°)) and bimodal orientations with two equal sized peaks (e.g. 130°/275°) are also indicated. Tests were performed on August 25, 26, 27, 30, and September 3, 4, 5, 8, 9, 10. dis = disorientation (mostly very low activity); '0' = no activity; '-' = not tested.

ID	Dir., Conc.	#	Nightly modal directions
<i>Experimentals</i>			
14RRG	141°, 0.569	6	50°, 140°, 105°, -, 140°, 240°, -, 180°, -, 130°/275°
14RRB	117°, 0.684	5	95°, 120°/290°, 170°, -, 90°, 60°, -, 180°, -, dis
7RGR	195°, 0.822*	5	dis, -, 205°, 120°, -, dis, 210°, 220°, -, 200°
7RGG	192°, 0.645	6	225°, -, 180°, 90°, -, 150°, 230°, 235°, -, 230°/80°
11RGB	135°, 0.817*	5	130°, -, 0, 105°, -, 210°, -, 120°, dis, 130°
11RBR	89°, 0.867*	4	130°, -, 45°, 95°, -, dis, -, 85°/(255°), dis, dis
18RBG	196°, 0.439	7	35°, 190°, -, 230°, 170°, 230°, -, -, 245°, 95°/(225°)
18RBB	172°, 0.377	7	105°, 260°, -, 185°, 120°, 200°, -, -, 270°, 75°
6GRR	179°, 0.412	4	100°, -, 210°, 285°, 150°, -, dis, 45°/310°, dis, -
6GRG	157°, 0.761	5	dis, -, 135°, 155°, 110°, -, 165°, 235°/(90°), dis, -
5GRB	164°, 0.846*	6	-, 210°, 170°, 195°, -, 115°, 135°, 160°, -, dis
5GGR	75°, 0.644	3	-, 0, 95°/230°, 90°/(225°), -, 0°, dis, 310°/165°, -, 120°
<i>Controls</i>			
2GGB	184°, 0.861**	7	150°, -, 225°/(45°), 195°, -, 180°, 180°, 220°, 135°, dis
2GBR	158°, 0.480	5	0, -, dis, dis, -, 150°, 230°, 140°, 160°, 10°
8GBG	144°, 0.821**	7	0, -, 195°, 165°/(50°), 140°, 105°, 185°, 105°, -, 115°
8GBB	188°, 0.723*	7	95°/(270°), -, 170°, 190°, 210°, 210°, 165°, 255°/(75°), -, dis
17BRR	170°, 0.735*	7	60°, 185°, 210°, -, 140°, 165°, -, 195°, -, 180°
17BRG	137°, 0.720*	6	110°, 135°, dis, -, 90°, 140°, -, 240°, -, 150°
4BRB	130°, 0.758*	6	150°, 200°, -, 80°, 135°, dis, -, 140°, 80°, dis
4BGR	80°, 0.409	8	195°, 125°, -, 120°, 255°, 45°/(185°), -, 40°, 40°, 50°
13BGG		1	dis, -, 0, 125°, -, dis, 0, dis, dis, 0
13BGB	157°, 0.605	6	dis, -, 150°, 75°, -, 105°, dis, 180°, 190°, 240°
3BBR	173°, 0.724*	6	-, 165°, 250°/(350°), 130°, -, 210°, 175°, 120°, dis, -

DISCUSSION

In this study, the birds developed a south-south-east migratory direction which deviated from due south (away from celestial rotation) without access to any meaningful magnetic information in the pre-migratory period. The experimental group showed a slightly lower (but not significantly so) directional concentration, which may have been influenced by the chaotic magnetic field. Thus, the conclusion that

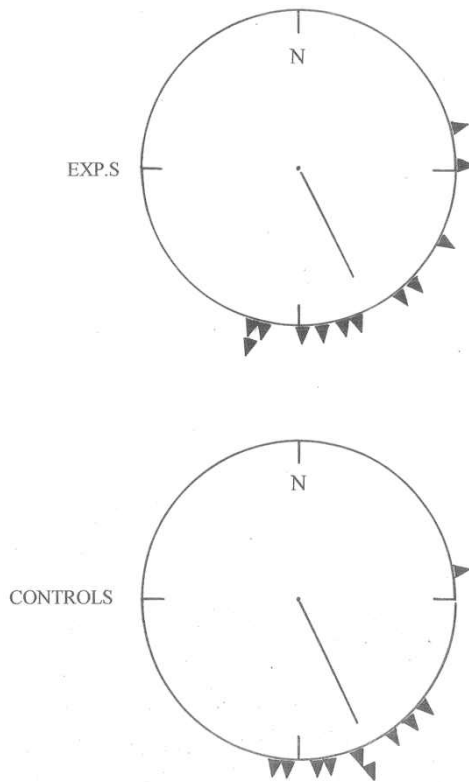


Fig. 2. — The migratory orientation of whitethroats, *Sylvia communis*, with (controls) or without access (experimentals) to meaningful geomagnetic information in the pre-migratory phase. Circular distributions and grand mean vectors of the experimentals and controls, respectively, are 153° , 0.788^{***} ($N = 12$, upper figure) and 154° , 0.872^{**} ($N = 10$, lower figure). Each triangle represents the sample mean direction of an individual bird displaying directed activity on at least 3 and up to 8 nights.

the magnetic field is crucial in the development of the inherited migration direction (WEINDLER et al. 1996, 1997; WILTSCHKO et al. 1998; WILTSCHKO & WILTSCHKO 1999, 2003) may be premature. Our study indicates that, when natural celestial cues are available in the pre-migratory period, it is possible to establish the appropriate migratory direction away from due south.

The northwest European whitethroat population is split by a weak migratory divide somewhere in eastern Denmark (ZINK 1973). The general direction shown by the whitethroats in this study corresponds to that observed in birds from east of this divide. Endelave lies closely or slightly to the west of this divide (i.e. birds are expected to migrate south-west). However, no long-distance recoveries (> 100 km) exist for birds ringed in Denmark as nestlings or as breeding adults to confirm the exact position of the divide (Ring recoveries at Zoological Museum, University of Copenhagen). The south-south-east direction observed in this study is unlikely to be caused or influenced by any local anomaly. Several hundred experiments have been

Table 2.

Components x , y and z (where x is the pointing toward geomagnetic north, y toward east and z is the vertical component, positive downward) of the magnetic field created by the bar magnets (in Gauss, G) in the experimental cages when magnetic north of the horizontal bar magnets was pointing west (see Fig. 1). The natural geomagnetic field at the test site is 0.48 G (48 000 nT) ($x = 0.16$ G, $y = 0$ G, $z = 0.45$ G).

Distance to cage centre (cm)	- 20	- 15	- 10	- 5	0	5	10	15	20
<i>5 cm above sticks; along west– east stick</i>									
X	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Y	3.6	6.7	- 11.6	- 10.6	12.2	- 10.6	- 11.6	6.7	3.6
Z	- 2.5	- 10.8	- 19.8	16.5	0.0	- 16.5	19.8	10.8	2.5
<i>5 cm above sticks; along south– north stick</i>									
X	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Y	- 0.6	- 0.8	- 0.6	3.4	12.2	3.4	- 0.6	- 0.8	- 0.6
Z	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>5 cm above bottom; along west– east axis</i>									
X		0.0	0.0	0.0	0.0	0.0	0.0	0.0	
Y		- 0.2	- 0.9	- 1.0	- 0.8	- 1.0	- 0.9	- 0.2	
Z		1.4	1.1	0.3	0.0	- 0.3	- 1.1	- 1.4	
<i>5 cm above bottom; along south– north axis</i>									
X		0.0	0.0	0.0	0.0	0.0	0.0	0.0	
Y		- 0.5	- 0.7	- 0.8	- 0.8	- 0.8	- 0.7	- 0.5	
Z		0.0	0.0	0.0	0.0	0.0	0.0	0.0	

performed with other species, in particular redstart *Phoenicurus phoenicurus* and pied flycatcher *Ficedula hypoleuca*, at Endelave following trapping on and displacement from Christiansø (300 km to the east). These birds mostly oriented southwest, though often after showing some initial southeast orientation, which could be interpreted as a compensatory reaction (pers. obs.). Furthermore, in these experiments, the directional preference was in several experiments changed by changing the direction of magnetic north using coils (pers. obs.). Hence, the observed migration direction can most likely be considered as the outcome of the innate migration programme, and the observed pattern of orientation in the control group is appropriate for considering the question whether or not the presence of a magnetic field is necessary for the setting of a migratory direction that deviates from due south.

According to WEINDLER et al. (1996) information is transferred from the magnetic compass to the celestial compass during the pre-migratory period: the population-specific migration course is coded with respect to the magnetic field alone as a deviation from the basic direction away from celestial rotation (i.e. south) and possibly the innate magnetic compass information does not specify any particular direction but only a deviation from the basic course. Our results do not support this view.

Several explanations can be found for the discrepancies. Earlier studies have exposed birds to limited celestial information, consisting of a simple planetarium starry sky with 16 stars that were not rotating while birds were tested. This limited 'celestial' information may have been insufficient for the birds to develop their innate migratory direction.

Other reasons include the possibility that the information from the geomagnetic field is already obtained in the nest as suggested by ALERSTAM & HÖGSTEDT (1983). However, MUHEIM et al. (2006) pointed out several issues questioning such an interpretation of the experiments by ALERSTAM & HÖGSTEDT (1983), and most other studies indicate that migratory orientation is developed later in the actual pre-migratory period. The experiments by WEINDLER et al. (1996) were based on 4-6 day-old nestlings, but they were not exposed to a rotating '16-star-sky' until mid July.

Caution is probably needed in the interpretation of results from studies of innate migration directions since significant deviations from the expected standard direction are shown in many funnel studies even with access to magnetic information. Pied flycatchers, *Ficedula hypoleuca*, showed south-east orientation in early autumn (BECK & WILTSCHKO 1982, BINGMAN 1984) as did goldcrests, *Regulus regulus* (WEINDLER 1994). In both species the standard direction is southwest. Also, there is a general north-west/south-east-axis of orientation in several North American birds (e.g. BINGMAN 1983, ABLE & CHERRY 1986, ABLE & ABLE 1995) with a standard axis north-east/south-west, as shown by ring-recoveries.

ACKNOWLEDGEMENTS

Thanks to Fritz Primdahl for help with measuring the magnetic fields and to Jette Andersen for linguistic suggestions.

REFERENCES

- ABLE K.P. & ABLE M.A. 1995. Interactions in the flexible orientation system of a migratory bird. *Nature* 375: 230-232.
- ABLE K.P. & CHERRY J.D. 1986. Mechanisms of dusk orientation in white-throated sparrows (*Zonotrichia albicollis*): Clock-shift experiments. *Journal of Comparative Physiology (A)* 159: 107-113.
- ALERSTAM T. & HÖGSTEDT G. 1983. The role of the geomagnetic field in the development of birds' compass sense. *Nature* 306: 463-465.
- BATSCHELET E. 1981. Circular statistics in biology. *New York: Academic Press*.
- BECK W. & WILTSCHKO W. 1982. The magnetic field as reference system for the genetically encoded migratory direction in Pied Flycatchers (*Ficedula hypoleuca* Pallas). *Zeitschrift für Tierpsychologie* 60: 41-46.
- BINGMAN V.P. 1983. Magnetic field orientation of migratory Savannah Sparrows with different first summer experience. *Behaviour* 87: 43-53.
- BINGMAN V.P. 1984. Night sky orientation of migratory pied flycatchers raised in different magnetic fields. *Behavioral Ecology and Sociobiology* 15: 77-80.
- EMLÉN S.T. 1970. Celestial rotation: Its importance in the development of migratory orientation. *Science* 170: 1198-1201.
- GWINNER E. & WILTSCHKO W. 1978. Endogenously controlled changes in migratory direction of the Garden Warbler, *Sylvia borin*. *Journal of Comparative Physiology (A)* 125: 267-273.

- HELBIG A., BERTHOLD P. & WILTSCHKO W. 1989. Migratory orientation of Blackcaps (*Sylvia atricapilla*): Population-specific shifts of direction during the autumn. *Ethology* 82: 307-315.
- MOURITSEN H. & LARSEN O.N. 1998. Migrating young pied flycatchers, *Ficedula hypoleuca*, did not compensate for geographical displacements. *Journal of Experimental Biology* 201: 2927-2934.
- MUHEIM R., MOORE F.R. & PHILLIPS J.B. 2006. Calibration of magnetic and celestial compass cues in migratory birds — a review of cue-conflict experiments. *Journal of Experimental Biology* 209: 2-17.
- RABØL J. 1970. Transformation of colour degrees to number of jumps using the Emlen orientation technique. *Dansk Ornithologisk Forenings Tidsskrift* 64: 118-126.
- STEPHENS M.A. 1972. Multisample tests for the von Mises distribution. *Journal of the American Statistical Association* 67: 456-461.
- WEINDLER P. 1994. Wintergoldhähnchen (*Regulus regulus*) besitzen einen inklinationskompass. *Journal für Ornithologie* 135: 620-622.
- WEINDLER P., BAUMETZ M. & WILTSCHKO W. 1997. The direction of celestial rotation influences the development of stellar orientation in young Garden warblers (*Sylvia borin*). *Journal of Experimental Biology* 200: 2107-2113.
- WEINDLER P., WILTSCHKO R. & WILTSCHKO W. 1996. Magnetic information affects the stellar orientation of young bird migrants. *Nature* 383: 158-160.
- WILTSCHKO R., MUNRO U., FORD M., WILTSCHKO W. 2001. Orientation in migratory birds: time-associated relearning of celestial cues. *Animal Behaviour* 62: 245-250.
- WILTSCHKO R. & WILTSCHKO W. 1995. Magnetic orientation in animals. *Berlin, Heidelberg: Springer-Verlag*.
- WILTSCHKO R. & WILTSCHKO W. 1999. Celestial and magnetic cues in experimental conflict, pp. 988-1004. In: Adams N.J. & Slotow R.H., Edits. Proceedings of the 22nd International Ornithological Congress, Durban. *Johannesburg: Birdlife South Africa*.
- WILTSCHKO R. & WILTSCHKO W. 2003. Mechanisms of orientation and navigation in migratory birds, pp. 433-456. In: Berthold P. et al., Edits. Avian migration. *Berlin, Heidelberg, New York: Springer-Verlag*.
- WILTSCHKO W., WEINDLER P. & WILTSCHKO R. 1998. Interaction of magnetic and celestial cues in the migratory orientation of passerines. *Journal of Avian Biology* 29: 606-617.
- ZINK G. 1973. Der Zug europäischer Singvögel. 1. Lieferung. *Möggingen: Vogelzug Verlag*.