



Autumn migratory orientation and displacement responses of two willow warbler subspecies (*Phylloscopus trochilus trochilus* and *P. t. acredula*) in South Sweden

Mihaela Ilieva^{a,c,*}, David P.L. Toews^b, Staffan Bensch^c, Christoffer Sjöholm^c, Susanne Åkesson^c

^a Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin St., 1113 Sofia, Bulgaria

^b Department of Zoology and Biodiversity Research Centre, University of British Columbia, 6270 University Blvd., Vancouver, B.C., V6T 1Z4 Canada

^c Department of Biology, Centre for Animal Movement Research, Lund University, Ecology Building, SE-223 62 Lund, Sweden

ARTICLE INFO

Article history:

Received 6 April 2012

Received in revised form 20 August 2012

Accepted 21 September 2012

Keywords:

Displacement

Genetic differences

Migratory divide

Orientation

Subspecies

Willow warbler

ABSTRACT

Topography and historical range expansion has formed a so-called migratory divide between two subspecies of willow warbler (*Phylloscopus trochilus*) in central Scandinavia. The autumn migratory directions of individuals assigned molecularly to both subspecies and possible hybrids were recorded using orientation cage experiments in southwest and southeast Sweden. We found pronounced differences in willow warblers' orientation in respect to genotype. The mean directions registered in the control experiments were in accordance with the ringing recoveries and analyses of stable isotopes for Scandinavian willow warblers. With the same individuals we performed displacement experiments between both sites. They resulted in non-significant orientation, which could be explained by the intermediate distance of the displacement or reactions to housing, transportation and location. On a separate set of birds we tested whether stress following transportation could explain the disorientation and found that orientation before and after transport was unchanged. Experimental studies of effects of intermediate displacements across longitudes and studies of orientation of hybrid individuals in the zones of migratory divides are crucial for understanding the mechanisms underlying orientation behaviour. Our work further stresses the importance of knowing the migration genotype of a particular bird under study, in order to correctly evaluate expected migration routes.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Despite extensive research in avian migration and orientation there are still many unanswered questions regarding the migratory programme of birds. Migratory directions of bird populations may reflect their historical range expansion (Ruegg and Smith, 2002), but at the same time migratory orientation is a very flexible trait, subject to fast microevolutionary changes (Berthold et al., 1992). As a result of topography and historical range expansion in many bird species so-called migratory divides have formed in Europe, separating the populations flying southeast or southwest in autumn (e.g. Bensch et al., 1999; Fransson and Hall-Karlsson, 2008; Hedenström and Pettersson, 1987; Procházka et al., 2008;

Zink, 1973). In these zones of secondary contact hybrid individuals might exhibit intermediate migratory directions, as suggested by cross-breeding experiments with hand-raised migrants (Helbig, 1991). Differences in migratory behaviour seem to be the result of selection on relatively few loci and thus it is not surprising that the genome wide separation is typically weak between populations showing different migratory directions (Bensch et al., 1999, 2002, 2006b, 2009; Buerkle, 1999; Helbig, 1994, 1996, 2003). The Scandinavian willow warbler (*Phylloscopus trochilus*) is an example where low genetic differentiation between the two subspecies (*P. t. trochilus* and *P. t. acredula*) is associated with a pronounced migratory divide and a contact zone in Central Sweden (e.g. Bensch et al., 1999, 2006b). The nominate subspecies *P. t. trochilus* breeds mainly south of 61°N while *P. t. acredula* is widespread north of 63°N and between these latitudes they form a hybrid zone (Bensch et al., 2002). On the basis of ringing recoveries it has been shown that both subspecies of Scandinavian willow warblers have different migratory routes – towards southwest for *trochilus* and south-southeast for *acredula* (Bensch et al., 1999; Hedenström and Pettersson, 1987). Corresponding differences in the wintering grounds are also reflected in the stable isotope signatures of feathers collected in

* Corresponding author at: Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Gagarin St., 1113 Sofia, Bulgaria. Tel.: +359 2 8736137; fax: +359 2 8705498.

E-mail addresses: mihaela.ilieva@gmail.com (M. Ilieva), toews@zoology.ubc.ca (D.P.L. Toews), Staffan.Bensch@biol.lu.se (S. Bensch), christoffer.sjoholm@email.com (C. Sjöholm), Susanne.Akesson@biol.lu.se (S. Åkesson).

Europe and Africa (Bensch et al., 2006a; Chamberlain et al., 2000). *P. t. rochilus* winters mainly in Western Africa, while *acredula* are wintering in eastern and southern parts of the continent. Using molecular methods Bensch et al. (2002, 2009) found clear differences between northern and southern birds in allele frequencies of two AFLP-derived markers, i.e. AFLP-WW1 and AFLP-WW2. In contrast, they were found to be nearly genetically indistinguishable in mitochondrial DNA and several microsatellite loci (Bensch et al., 1999, 2006b, 2009). The AFLP-WW1 locus is an anonymous non-coding autosomal region (Bensch et al., 2002; Lundberg et al., 2011), whereas the AFLP-WW2 locus could be linked to a gene encoding for intraspecific variation of the migratory programme, based on a correlation with differences in nitrogen isotopes at broad geographic scales (Bensch et al., 2009).

In order to confirm the patterns observed in previous studies, this time with the addition of genetic data, we recorded the autumn migratory directions of both willow warbler subspecies and possible hybrids in two different parts of southern Sweden with orientation cage experiments. Our expectations were that *P. t. trochilus* would choose southwestern direction, *P. t. acredula* would orient in a south-southeastern direction and the hybrid individuals would show intermediate directions. We also aimed to investigate some of the factors that can influence the birds' orientation behaviour, such as the accessibility to orientation cues, fat level and geographical location. The subspecies affiliation of the willow warblers, but also the geographical position of both locations, with one situated inland (Lake Krankesjön, SW, Sweden) and the other located in front of an ecological barrier, the Baltic Sea (Öland, SE, Sweden), was expected to influence the directions chosen by migrants. The role of such ecological barriers on the behaviour of migratory birds has been shown in a number of studies (Åkesson et al., 1996; Biebach et al., 2000; Bruderer and Jenni, 1990; Sandberg, 2003; Zehnder et al., 2002). Often the decision for continuing migration, performing flights in reverse directions or orienting in directions along the coast lines depends on time of the day/night, weather and/or body condition of the migrants (Åkesson et al., 1996; Bruderer and Liechti, 1998; Richardson, 1978; Sandberg, 2003; Sandberg and Moore, 1996). Birds with lower fuel reserves more frequently exhibit reverse orientation in Emlen funnels (Bäckman et al., 1997; Deutschlander and Muheim, 2009; Sandberg et al., 2002, but see Marchetti and Zehndjiev, 2009) particularly when experiments are carried out along sea coasts (Åkesson et al., 1996; Bruderer and Liechti, 1998) compared to experiments at inland sites (Åkesson, 1999). Therefore, we expected, willow warblers caught at the coastal location and leaner birds to be more prone to show reverse directions compared to individuals tested at the inland site.

Another important factor that can greatly influence birds' orientation and motivation to migrate is the ability to see the celestial cues in the sky (Åkesson, 1994; Åkesson and Bäckman, 1999; Moore, 1987). We tested this in the willow warbler system by performing experiments in simulated overcast conditions to determine how important the celestial cues are for the willow warblers and if this species can use only the Earth's geomagnetic field for orientation. During the last few decades of research substantial evidence has shown the importance geomagnetic information in the processes of orientation and navigation in various animal species (see review of Åkesson, 2003; Freake et al., 2006; Wiltschko and Wiltschko, 1995). The geomagnetic field seems to play a key role in determining and maintaining the migratory direction in birds, together with other celestial compasses (Muheim et al., 2006a; Wiltschko and Wiltschko, 1972), but still the use of a magnetic map have been confirmed in very few species of animals (e.g. Boles and Lohmann, 2003; Fischer et al., 2001; Wu and Dickman, 2012; Phillips et al., 1995). Often, deprivation from one or more important cues can lead to

disorientation of the experimental animals (e.g. Åkesson, 1993, 1994; Marchetti et al., 1998; Moore, 1986). In our experimental setup we used the simplest method to test the importance of the magnetic cues for willow warblers: we prevented the birds from acquiring celestial information by performing experiments under simulated overcast conditions at the place of capture as well as after the displacements. Our prediction was that the willow warblers would be less active and more disoriented under simulated overcast conditions than under natural sky with celestial cues available.

Another set of experiments was performed to investigate the abilities of willow warblers to recognize a middle-distance displacement (in our case ca. 200 km great circle route distance). We tested whether the birds changed their direction according to the displacement ("moving-goal-area", Rabøl, 1978) or kept a constant course relative to the expected wintering area ("clock-and-compass", Berthold, 1996). To study the effect of displacement we analysed only the experiments carried out with juvenile willow warblers. This decision was motivated from the difference in the migration experience of both age classes. By performing a meta-analysis of orientation cage experiments, Thorup and Rabøl (2007) have shown that even naïve first-year migrants in autumn can compensate to some degree for displacement under natural or planetarium starry skies. The orientation cage experiments carried out by Rabøl (1981) and Åkesson et al. (2005) and the studies of Thorup et al. (2011) also suggest that juvenile birds possess the ability to correct for displacement in some circumstances. The responses to geographical or simulated displacements have been shown to vary extensively, from absence of compensation with no resulting shifts in orientation to full compensation (see reviews of Åkesson, 2003; Freake et al., 2006; Thorup and Rabøl, 2007). To test if stress might have influenced the results from displacements we also performed a short-distance (5–10 km) simulated displacement (i.e. individuals were caught and tested in the sample location) with another group of willow warblers.

In conclusion our study aimed to: (1) confirm the previous ringing data on the willow warbler migratory divide using orientation experiments with individuals genetically identified as belonging to one or the other subspecies; (2) test for differences in the orientation of the birds at two different sites, inland and coastal; (3) compare orientation under clear or artificially overcast sky; (4) compare orientation after a middle-distance E–W displacement; and (5) control for transportation stress by comparing orientation before and after a simulated displacement.

2. Methods

2.1. Study sites, experimental and displacement procedures

During the autumn of 2009, we performed orientation cage experiments with willow warblers at two different localities: at Stensoffa Ecological Field Station (55°41'N 13°26'E) in southwest Sweden (SW-inland-site) and at the southern tip of the island of Öland (56°13'N 16°24'E) in southeast Sweden (SE-coast-site), to examine their migratory direction. From 25 to 29 August we captured 47 willow warblers in mist-nets at Lake Krankesjön (1.5 km northeast from Stensoffa Station; two other birds were captured two weeks earlier) and tested them in modified Emlen funnels (Emlen and Emlen, 1966), allowing the birds to see approximately 160° of the sky (Åkesson, 1994). On 4 September we transported 36 of the willow warblers by car to Ottenby Bird Observatory, situated at the island of Öland and tested them again at an open area, 2.5 km north-northeast from the observatory. We chose this site in order to avoid light from the lighthouse situated at the southernmost tip of the island, which could influence the bird's responses. After the

release of the first group of willow warblers, we tested another 48 willow warblers caught at Ottenby Bird Observatory between 10 and 15 September. For this set of experiments we had to use another experimental site, located at 4 km north-northeast from the Ottenby Station for two nights, due to disturbance from grazing animals at our original experimental site. After the experiments at the SE-coast-site, on 16 September, we transported 41 of the willow warblers to the SW-inland-site. There we performed orientation experiments and released the birds near the station after the cage experiments were finished. During the experimental period willow warblers at both study sites were kept indoors for 1–15 days (two birds were kept longer, for 22 and 30 days, respectively) with free access to meal-worms, *Tenebrio molitor*, and fresh water with added vitamins. Willow warblers that were feeding properly in captivity were kept for further studies, while the others were released if they were losing weight.

At each test site, as well as after the displacements, we performed orientation experiments under natural sky conditions (cloud cover 0–6/8; in one night 8/8) and simulated overcast conditions. In the later case we covered the top of the cage with a 2 mm diffusing Plexiglas sheet. The majority of the experiments were performed in the same sequence and similar time interval between the different treatments, with small variations due to unfavourable weather conditions. In 96% of the cases we conducted a control test in the day of capture. A second control test (with 75% of the willow warblers) was performed on the third day after capture. Birds were tested under simulated overcast 5–7 days after the first control test. In 16 cases the sequence of second control test and overcast test was changed. Some birds (8 at SW-inland-site and 1 at SE-coast-site), mostly representing individuals that did not eat sufficiently, were tested only once and were then released. After the displacement the birds were tested for the first time at earliest on the second night after arrival, in most cases first under clear sky and then under simulated overcast. However, due to weather conditions and limited time 50% of the birds displaced to SE-coast-site and 8% of the birds displaced to SW-inland-site were tested under simulated overcast first.

At capture and before each orientation test was performed we registered the fat score, according the visual classification scale (0–6) by Pettersson and Hasselquist (1985), and weight (to the nearest 0.1 g with a Pesola spring-balance) of the experimental birds. In order to test birds in migratory condition we mainly chose willow warblers with fat scores of at least 3 and which had already finished their moulting. Birds with fat score 3 or less were classified as lean in the analyses. Eight willow warblers caught at SE-coast-site had fat scores below 3 at the capture. As it was the end of the migratory season for willow warblers and because of the location of the capture site near the coast, we considered that all these birds were in migratory condition. The willow warblers were aged according to Svensson (1992). Only six of the experimental willow warblers were adult birds, while the rest of the birds were juveniles ($n=91$).

To address whether the results of the orientation experiments after displacements (see below) could be a result of stress induced by captivity or transport, in autumn 2010 between 18 August and 5 September, one of us (D.P.L.T.) performed another series of orientation experiments at SW-inland-site. In this case, 39 willow warblers were captured on migration in the period 18–29 August and were tested under clear and simulated overcast conditions shortly after sunset. On a later day these individuals were driven by car for approximately one hour (~100 km) in areas (1–15 km) surrounding the ecological station. Hence, these individuals were experiencing similar holding and transport conditions as those individuals that were displaced in 2009, however they were tested again at the same site.

Ethical permissions to perform the experiments and to sample blood for genetic analyses were given by Malmö/Lunds djurförsöksetiska nämnd (No. M27-10; M94-08). Permissions were given from Naturvårdsverket and the Swedish Ringing Centre for capturing birds.

2.2. Genetic analyses

Blood samples were taken before releasing the willow warblers following their final orientation experiment or at least two days before the orientation experiments, in order to avoid additional stress to the birds. DNA was isolated by phenol-chloroform extraction (Sambrook et al., 1989) and diluted to 5 ng/ μ l working concentration. The genetic typing of two AFLP-derived markers, AFLP-WW1 and AFLP-WW2, was outlined in Bensch et al. (2002, 2009). Both these loci exhibit two alleles that have very different frequencies in southern and northern Sweden. For each locus we scored the birds as homozygous southern (S), heterozygous (H) and homozygous northern (N), respectively.

2.3. Data evaluation and statistical analyses

Each individual's orientation was recorded on thermo-paper and evaluated by activity and concentration indexes according to Mouritsen (1998; first developed by Rabøl, 1970). Both indexes are defined on a 0–4 scale, where activity represents number of scratches per hour, with $0 < 30$ scratches and $4 > 2000$ scratches, and concentration as the angle within which the mean direction without doubt lies, with $1^\circ < 45^\circ$ and $4 \pm 0-5^\circ$. The lower limit of activity, below which we classified an individual as showing “no activity”, was set at 30 registrations in our tests. The mean activity per group was calculated on the basis of all tests, including those with no or low activity (<30 claw marks), whereas the mean concentration index was calculated excluding those tests. For comparisons of activity and concentration we used Mann–Whitney *U*-test and Sign test (Siegel and Castellan, 1988). Experiments where birds were inactive or showed disorientation (Tables 1 and 2) were excluded from analyses of orientation. The mean individual directions were then used in the group analyses. In the cases with axial orientation, when two peaks of activity are observed and the difference between the mean opposite directions were not more than $180 \pm 30^\circ$ (Tables 1 and 2), we used the direction where the majority of the bird scratches were registered. The mean orientation of the different groups was calculated with circular statistics and we used the Rayleigh test to check if the mean orientation differed from a random distribution (Batschelet, 1981). For analyses of orientation, activity and concentration after displacements we used 1st year birds only, while the rest of the analyses included also the adult birds. The group comparisons were done with Watson's U^2 -test (Batschelet, 1981) and Moore's paired test (Zar, 1999). We used 95% Confidence Interval (Batschelet, 1981) to test if the mean orientation differed from the position of the Sun during the experiments. We analysed the results after the one-hour driving experiment as the angular deviation from the initial orientation of each individual, if an individual displayed significant mean orientation in both tests.

3. Results

3.1. Genetic analyses and morphological traits

According to both AFLP-derived markers southern, *trochilus* individuals were more abundant during migration through the SW-inland-site, while at the SE-coast-site we registered a greater variety of birds with both *trochilus* and *acredula* genetic markers (Fig. 1). Willow warblers with only southern alleles (S/S) comprised

Table 1

Number of willow warblers captured at the SW-inland-site (Stensoffa Ecological Field Station) and tested in orientation cages in autumn 2009. For each group are given: mean activity (A), concentration (C), mean direction (α), vector length (r) and level of significance (p). "I" refers to the first tests, and "II" to the second tests. For axial distributions the axial mean orientation (α_1/α_2), vector length (r_2) and level of significance (p_2) are given.

	Total	Inactive	Mean A	Disoriented	Mean C	Axial	Included	α (α_1/α_2)	r (r_2)	p (p_2)
Control (I) all	49	3	1.67	2	2.67	13	41	261°	0.34	0.01
Control (I) WW2 – S	35	2	1.68	1	2.64	8	29	264°	0.39	0.01
Control (I) WW2 – H	10	1	1.40	0	3.00	4	9	14°/194°	0.30	0.45
Control (I) WW2 – N	2	0	1.50	0	3.00	0	2	93°/273°	0.91	0.19
Control (I) WW1 – S/WW2 – S	26	1	1.89	0	2.72	6	24	262°	0.37	0.04
Control (II) all	39	2	1.58	3	2.53	3	30	261°	0.38	0.01
Simulated overcast	37	2	1.76	4	2.00	11	30	14°	0.21	0.26
Displaced to the SE-coast-site, control	32	0	2.38	4	2.66	10	28	105°/285°	0.20	0.33
Displaced to the SE-coast-site, simulated overcast	32	7	1.16	5	2.32	4	20	40°/220°	0.37	0.07

Table 2

Number of willow warblers captured at the SE-coast-site (Ottenby Bird Observatory) and tested in orientation cages in autumn 2009. For each group are given: mean activity (A), concentration (C), mean direction (α), vector length (r) and level of significance (p). "I" refers to the first tests and "II" to the second tests. For axial distributions the axial mean orientation (α_1/α_2), vector length (r_2) and level of significance (p_2) are given.

	Total	Inactive	Mean A	Disoriented	Mean C	Axial	Included	α (α_1/α_2)	r (r_2)	p (p_2)
Control (I) all	48	10	1.38	0	2.82	6	36	171°/351°	0.29	0.04
Control (I) WW2 – S	7	1	1.57	0	2.67	1	6	34°/214°	0.55	0.16
Control (I) WW2 – H	4	1	1.75	0	2.33	0	3	1°/181°	0.48	0.49
Control (I) WW2 – N	35	7	1.31	0	2.85	4	26	158°/338°	0.35	0.04
Control (I) WW1 – N/WW2 – N	17	4	1.29	0	3.08	3	13	164°/344°	0.29	0.34
Control (II) all	35	7	1.71	0	2.93	2	28	304°	0.37	0.02
Simulated overcast	46	14	1.09	2	2.34	7	29	152°/332°	0.15	0.54
Displaced to the SW-inland-site, control	39	7	1.64	2	2.38	6	30	253°	0.19	0.34
Displaced to the SW-inland-site, simulated overcast	39	7	1.54	4	2.03	6	28	141°/321°	0.21	0.28

almost half (45%) of birds caught at the SW-inland-site, but only 7% of those caught at the SE-coast-site. In contrast, "pure" northern birds (N/N) were found at the SE-coast-site (37%), but not at the SW-inland-site. If only the AFLP-WW2 is taken into consideration, which is a genetic marker that previous research suggests may be linked to migratory behaviour, the percentage of southern homozygotes was 60% at the SW-inland-site and the frequency of northern homozygotes was 76% at the SE-coast-site. Willow warblers heterozygous for WW2 were more often caught at the SW-inland-site (38%) than at the SE-coast-site (9%).

3.2. Orientation under natural sky and simulated overcast at the place of capture

Under natural sky conditions the willow warblers captured at the SW-inland-site and tested for the first time showed mean orientation directed towards WSW (261°) (Fig. 2a; Table 1). This direction was significantly different from the position of the sun in the middle of the experimental hour (301.2°, $p < 0.05$). We analysed orientation of the experimental birds according to AFLP-WW2 marker in order to search for directional differences in willow warblers passing through the SW-inland-site (Fig. 2a). The small sample of active birds with WW2-H ($n = 9$) and WW2-N ($n = 2$) did however

not allow us to make more detailed analysis of their directions. Both groups showed axial orientation responses not significantly different from random (Table 1). The genetically southern individuals (WW2-S and those of the birds with WW1-S/WW2-S) were significantly oriented towards WSW, 264° and 262°, respectively (Table 1). In the second test under natural sky, the willow warblers were significantly oriented in the same mean direction as in the first test (Fig. 2c; Table 1). Individuals' orientation was also similar between the first and the second control tests (Moore's paired test: $R^2 = 0.16$, $p > 0.9$, $n = 26$).

The willow warblers caught and tested at the SE-coast-site showed axial mean orientation along a SSE–NNW (171°/351°) axis (Fig. 2b; Table 2). Analysed separately, the three groups of birds according to AFLP-WW2 also showed axial mean orientation (Table 2). The mean direction of the willow warblers with southern alleles was approximately SW–NE. Heterozygotes showed S–N axial orientation and the birds with northern alleles had SE–NW mean orientation. Only the northern willow warblers were significantly directed (Table 2) while the other two groups had small sample and their mean directions were not significant. When the birds were tested for the second time their orientation (304°) was significantly different from the first test (Watson's U^2 test: $U^2 = 0.65$, $p < 0.001$), but not from the direction of the

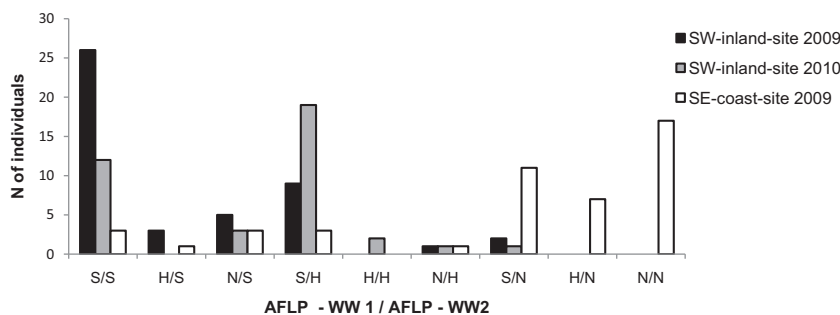


Fig. 1. Number of experimental willow warblers (*Phylloscopus trochilus*) according AFLP-derived WW1 and WW2 genetic markers (S – homozygous for southern alleles; N – homozygous for northern alleles; H – heterozygous, having both northern and southern alleles).

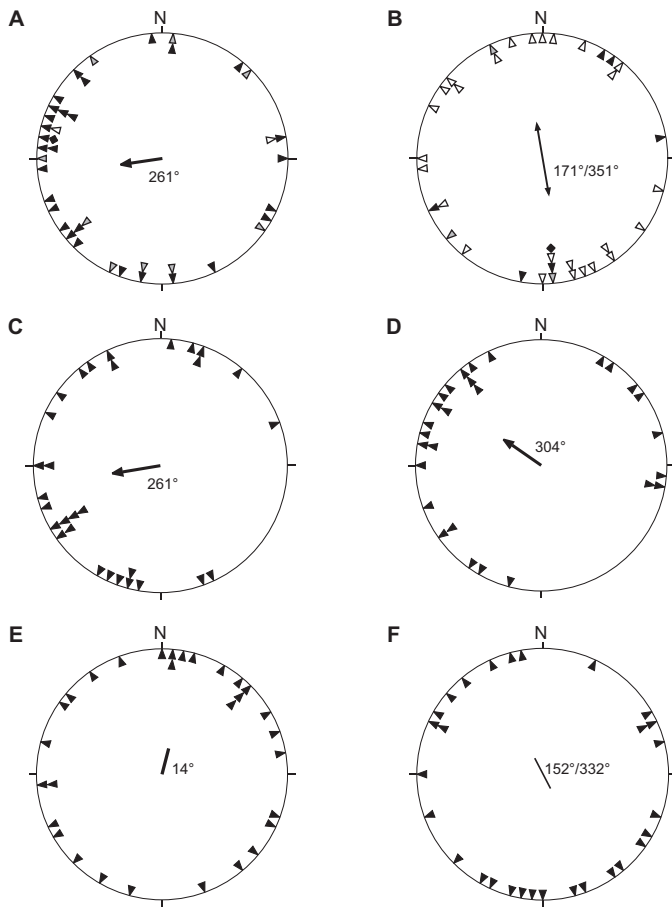


Fig. 2. Mean angle of orientation for willow warblers (*Phylloscopus trochilus*) tested at the SW-inland-site (left) and the SE-coast-site (right) in autumn. (A) and (B) Orientation under natural sky in first experiments; birds from southern (S), intermediate (H) and northern (N) type according to AFLP-WW2 marker are represented with black, grey and white triangles, respectively, while unidentified individuals are marked with diamonds; (C) and (D) orientation under natural sky conditions in the second experiments; (E) and (F) orientation under simulated total overcast. The arrow in each circular diagram represents the mean angle (α) and the length of the mean vector (r) relative to the radius of the circle ($r = 1$).

setting Sun (293.9° , $p > 0.05$) (Fig. 2d; Table 2). Moore's paired test did not show significant difference in individuals' orientation between the first and the second control tests ($R' = 0.70$, $p > 0.1$, $n = 22$).

The mean orientation of the willow warblers tested at the SW-inland-site and SE-coast-site under natural skies in the first experiments were significantly different from each other (Watson's U^2 test: $U^2 = 0.77$, $p < 0.001$).

Under simulated total overcast the willow warblers at both study sites failed to show significant mean orientation (Fig. 2e and f; Tables 1 and 2).

We did not find a significant difference in the mean orientation in the control experiments between fat and lean birds at SW-inland-site (fat: $\alpha = 271^\circ$, $r = 0.28$, $n = 24$, $p = 0.15$; lean: $\alpha = 252^\circ$, $r = 0.43$, $n = 17$, $p = 0.04$; Watson's U^2 test: $U^2 = 0.05$, $p > 0.5$) or at the SE-coast-site (fat: $\alpha_1/\alpha_2 = 2^\circ/182^\circ$, $r = 0.25$, $n = 10$, $p = 0.53$; lean: $\alpha_1/\alpha_2 = 167^\circ/347^\circ$, $r = 0.32$, $n = 26$, $p = 0.07$; Watson's U^2 test: $U^2 = 0.07$, $p > 0.5$) (Fig. 3).

3.3. Orientation after displacement and driving experiment

Displaced willow warblers failed to show significant mean orientation in experiments under natural sky conditions or in simulated overcast conditions (Fig. 4; Tables 1 and 2). In all cases,

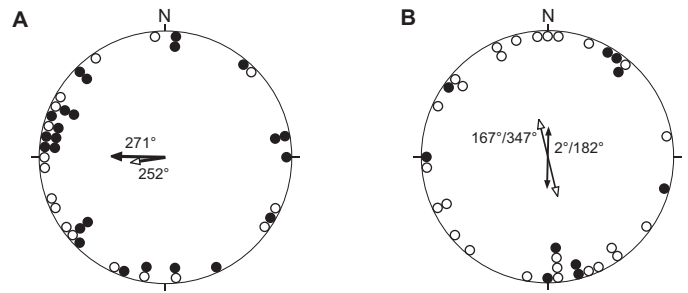


Fig. 3. Orientation of fat (black circles) and lean (white circles) willow warblers (*Phylloscopus trochilus*) tested at the SW-inland-site (left) and the SE-coast-site (right) under natural sky in first control experiments. For further information see Fig. 2.

except the willow warblers tested in simulated overcast at the SW-inland-site (Fig. 4c, where the distribution is totally dispersed), willow warblers showed non-significant axial orientation. Moore's paired test was used to compare individuals' orientation before and after the displacements. Birds displaced from SW-inland-site to SE-coast-site differed significantly in their orientation in the first control experiments at the two sites ($R' = 1.26$, $p < 0.01$, $n = 25$) while the willow warblers displaced in the opposite direction did not differ ($R' = 0.29$, $p > 0.5$, $n = 25$). In overcast conditions there was no difference in either group (SW to SE displaced group: $R' = 0.82$, $p > 0.1$, $n = 16$; SE to SW displaced group: $R' = 0.88$, $p > 0.1$, $n = 14$).

Moore's paired test did not show a significant difference in individuals' orientation before and after driving experiment either under clear sky ($R' = 0.59$, $p > 0.1$, $n = 35$) nor in simulated overcast ($R' = 1.02$, $p > 0.05$, $n = 14$). In the control experiments birds showed northwestern mean orientation (307° ; Fig. 5; Table 3) that was not different from the Sun's position in the middle of the experimental hour (300.1° , $p > 0.05$). There was also no correlation between orientation and genotype at WW2, as all groups showed NW mean orientation (Table 3). The analysis of individual deviation in the orientation after the driving from the initial response also showed that the mean direction before driving ($\alpha = 308^\circ$, $r = 0.33$, $n = 35$, $p = 0.02$) was not significantly different from the mean response direction after driving ($\alpha = 350^\circ$, $r = 0.31$, $n = 35$, $p = 0.03$; CI: $308-32^\circ$, $p > 0.05$)

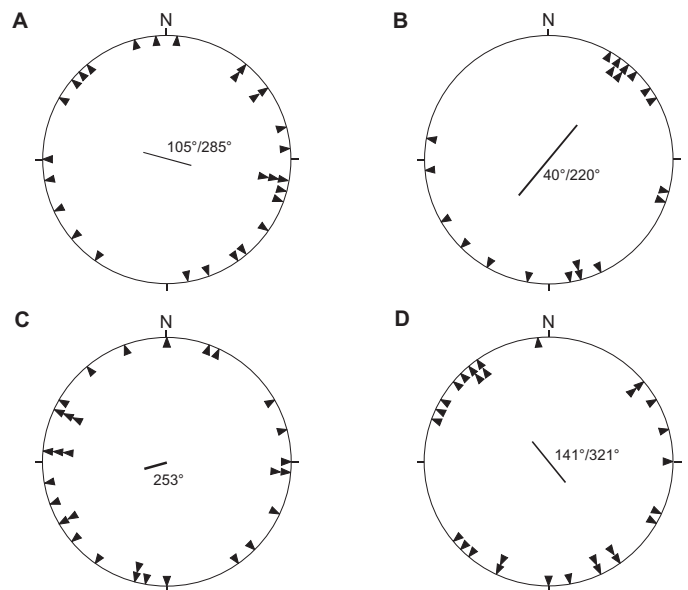


Fig. 4. Orientation of willow warblers (*Phylloscopus trochilus*) under natural clear skies (A, B) and simulated total overcast (C, D) after displacement to the SE-coast-site (left) and the SW-inland-site (right). For further information see Fig. 2.

Table 3
Number of willow warblers captured at the SW-inland-site and tested in orientation cages in autumn 2010. For each group are given: mean activity (A), concentration (C), mean direction (α), vector length (r) and level of significance (p). BD – test before drive; AD – test after drive.

	Total	Inactive	Mean A	Disoriented	Mean C	Axial	Included	α	r	p
Clear sky (BD) all	39	1	2.44	1	2.63	8	37	307°	0.36	0.008
Clear sky (BD) WW2 – S	15	0	2.20	1	2.73	5	14	306°	0.48	0.04
Clear sky (BD) WW2 – H	23	1	2.57	0	2.55	3	22	310°	0.25	0.25
Clear sky (BD) WW2 – N	1	0	3	0	3	0	1	300°		
Clear sky (AD) all	39	1	1.90	1	2.82	5	36	283°	0.45	<0.001
Simulated overcast (BD)	39	7	1.51	11	1.81	2	25	263°	0.31	0.09
Simulated overcast (AD)	39	6	1.54	8	2.03	3	24	316°	0.20	0.39

in clear sky tests (Fig. 5). Mean orientation under simulated overcast was not significantly different from random before and after the driving (Table 3).

3.4. Activity and concentration

Mean activity in the first control experiments was higher at the SW-inland-site in comparison with the SE-coast-site, but the difference was not significant (Mann–Whitney *U*-test: $U=993$, $p=0.16$; Tables 1 and 2). Mean concentration of both groups was similar (Mann–Whitney *U*-test: $U=846$, $p=0.78$; Tables 1 and 2). In simulated overcast the willow warblers at the SW-inland-site were significantly more active than the birds tested at the SE-coast-site (Mann–Whitney *U* test: $U=521$, $p=0.001$; Tables 1 and 2). The willow warblers at the SE-coast-site were also more often inactive in comparison to birds from the SW-inland-site (Tables 1 and 2). The difference in concentration in simulated overcast was not significant (Mann–Whitney *U* test: $U=449$, $p=0.14$; Tables 1 and 2).

In the first control experiments willow warblers showed significantly higher concentration than in simulated overcast at the SW-inland-site (sign test: $p=0.001$; Table 1), but at the SE-coast-site the difference was not significant (sign test: $p=0.21$; Table 2). Mean activity was not significantly different between control and overcast experiments at both locations (SW-inland-site: sign test: $p=0.79$; Table 1; SE-coast-site: sign test: $p=0.19$; Table 2).

After the displacement juvenile willow warblers showed higher activity in natural sky conditions compared to the first experiments performed at the original capture site. Birds displaced to the SE-coast-site had significantly higher activity (sign test: $p=0.02$), but not the group displaced in the opposite direction (sign test: $p=0.86$). In simulated overcast the willow warblers displaced to the SW-inland-site were more active after the displacement, but not significantly so (sign test: $p=0.23$). Birds displaced to the SE-coast-site showed significantly lower activity under simulated overcast after the displacement (sign test: $p=0.002$) and it was reduced by 50% compared to under clear skies.

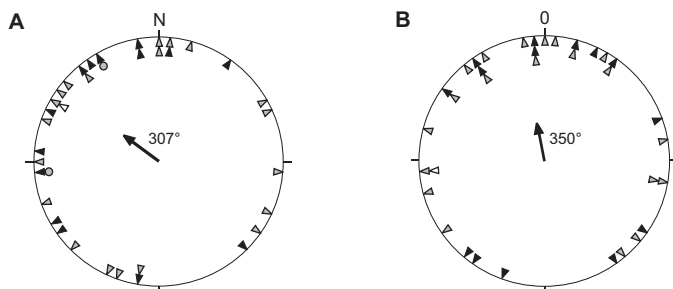


Fig. 5. Orientation of willow warblers (*Phylloscopus trochilus*) under natural clear skies before (A) and after (B) the car driving experiment. For details on colours and further information see Fig. 2. Circles represent individuals which failed to show a mean direction significantly different from random in the experiments after driving. The results after driving are given in angles of deviation from the initial response, setting the initial experiment as 0°.

4. Discussion

We found a marked difference in both genotype and orientation in willow warblers caught during their autumn migration and tested at the two sites in southern Sweden. As expected from the geographic distribution of the willow warblers subspecies and their temporal and spatial migration patterns (Bensch et al., 1999; Fransson and Hall-Karlsson, 2008; Hedenström and Pettersson, 1984), the proportion of birds with southern alleles was higher in the SW-inland-site while birds having northern alleles were more common in the SE-coast-site. Hence, the genetic data support that our sampling scheme was successful in obtaining two sets of birds originating from the two subspecies.

The mean orientation of willow warblers under natural skies also corresponded with the expected migratory directions of *trochilus* and *acredula* based on previous analyses of ringing recoveries (Bensch et al., 1999). In the SW-inland-site *trochilus* individuals dominated, and this is consistent with the mean WSW orientation. At this location one third of the experimental birds showed northwestern orientation, also coinciding with the direction of the setting sun, leading to a shift of the main direction to the west. Such phototactic response has previously been observed in orientation cage experiments with various passerine migrants (e.g. Åkesson, 1994; Sandberg, 1991). One possible explanation for this behaviour could be the fat level of the experimental birds. However, in our study we did not find a clear difference between fat and lean birds in this respect and other, and thus unknown factors could be behind this response.

At the SE-coast-site the willow warblers showed axial mean orientation. The majority of the individuals in this location carried northern alleles and their mean orientation was directed along a SE-NW axis. While we predicted a SSE for individuals at this site, in this case a considerable proportion of birds also showed reverse directions of orientation towards NW. This result is consistent with previous studies of migrants arriving at coastal locations, where reverse migration has often been registered in both free-flying birds as well as in cage experiments (e.g. Åkesson et al., 1996; Bäckman et al., 1997; Deutschlander and Muheim, 2009; Sandberg, 2003; Zehnder et al., 2002).

The reduced activity of the willow warblers at the SE-coast-site, in comparison with the SW-inland-site, especially in simulated overcast conditions, may be caused by the presence of an ecological barrier. In numerous previous studies it has been found that migrants tend to avoid direct crossing of open sea, especially in unfavourable weather conditions (Åkesson and Hedenström, 2000; Åkesson et al., 2001; Åkesson et al., 2002; Alerstam and Pettersson, 1977; Schmaljohann and Naef-Daenzer, 2011).

In our study the willow warblers did not show significant orientation under simulated overcast at either experimental site. The restricted ability to see the sky, especially in places where the correct orientation is of high importance, seems to influence the decision for migratory departures in willow warblers and their orientation. The experimental situation (especially in simulated overcast conditions) can restrict even further the abilities of birds

to orient in comparison with free-flying migrants at coastal sites (see Nievergelt et al., 1999).

We did not observe compensation for the displacements or significant mean orientation in either group of displaced willow warblers under clear sky or in simulated overcast conditions. The possible explanations for that could be a lack of important orientation cues and/or possibly too short interval (1–2 days) preceding the experiments at the new place. Prior to the experiments at the study locations, the experimental birds were not given the possibility to observe the setting sun. As the polarized light cues near the horizon at sunrise and sunset provide a primary calibration reference for the compass systems of migratory songbirds (Muheim et al., 2006b), the experimental birds were not able to recalibrate their compasses. Another reason for the lack of compensation after the displacement may be the distance of the displacements (ca. 200 km), much smaller than the long-distance displacements in the studies of Åkesson et al. (2005) and Thorup et al. (2007, 2011). Yet another possibility might be the lack of visibility to see stars at the site prior to experimentation, which has been shown to be important to songbirds in some displacements (Thorup and Rabøl, 2007). Furthermore, the differences between the magnetic parameters between both study sites were relatively small (Δ Inclination: $0^{\circ}17'$; Δ Declination: $1^{\circ}03'$; Δ Horizontal intensity: 295 nT; Δ Total field: 278 nT; as calculated for 01.01.2010 using WMM2010; <http://www.ngdc.noaa.gov/geomag/magfield.shtml>). In his review, Phillips (1996) considered that at intermediate distances (i.e. 10–50 km) the geomagnetic field is unlikely to be a reliable source of map information, because of local variations of the geomagnetic field parameters. It is possible that this distance is species-specific and it can differ depending on the size of the animal's range of movements. In the case of the willow warbler, which is a long-distance migrant, this distance could be larger and our displacement may fall within the range where the bird is not capable to use the geomagnetic cues for map information. The distance needed for reliable map information can also be increased when the access to orientation cues is reduced as in the case of orientation cage experiments (cf. Thorup and Rabøl, 2007).

A possible explanation for the lack of significant orientation after displacement might also be an effect of the transportation itself. Based on the experiments with homing pigeons it has been suggested that prevention of acquiring correct magnetic information during transportation can cause disturbances in their initial orientation (Kiepenheuer, 1978; Wiltschko and Wiltschko, 1981). Later experiments also with homing pigeons showed that the disorientation observed in those conditions was likely induced by stress from transportation and the birds' orientation was as good as in controls when they were injected with tranquillizer before transportation (Luschi et al., 1996). In our study, even if the birds were not tested immediately after the arrival, it is possible that stress induced by transportation, lasting several hours, could have had an effect during the next few days. However, in our attempt to partially address this factor with the driving experiment, where the birds would have experienced a similar transportation environment but were not displaced to another location, we did not observe a difference in the mean orientation before and after transportation. However, we could not rule out the possibility that stress was induced from changing the holding and testing locations, and not from the transportation itself.

The distinct ecological differences between both locations (coast vs. inland) may have confused the birds and increased noise in the data. The willow warblers from the two study sites responded in a different way to the southeast and southwest displacement with respect to activity and concentration. The birds displaced from the SW-inland-site to the SE-coast-site showed reduced activity and higher number of disoriented individuals under simulated overcast and higher activity in the clear sky experiments after the

displacement. In contrast, the group caught at the SE-coast-site and displaced in the opposite direction had increased activity in both clear sky and simulated overcast conditions. It is possible that the birds were able to recognise the presence or absence of the sea at the two sites and under poor visibility (simulated overcast) showed reduced or increased activity respectively.

In conclusion, this study has investigated the migratory behaviour of the Scandinavian willow warblers during their autumn migration. We found pronounced differences in willow warblers' orientation in respect to genotype. The mean directions registered in the control experiments at the two sites were in accordance with those expected from the ringing recoveries, but more individuals showed reverse directions at the SE-coast-site at the southernmost tip of the island of Öland. In simulated overcast we observed more scatter, non-significant orientation at both sites and reduced activity of the willow warblers at the SE-coast-site, in comparison with the SW-inland-site. The displacement experiments also resulted in non-significant orientation, which can possibly be explained with the intermediate distance of displacement or possible reactions to housing, transportation and type of location (coastal/inland). More generally, our observation of disorientation following displacement is consistent with a 'hard-wired' migration route, which is a central assumption of the migratory divide hypothesis (Irwin and Irwin, 2005), and implies that hybrid individuals inheriting an intermediate and potentially inferior migratory route may suffer a fitness loss as result. However, the temporal aspect of willow warbler migration, orientation abilities of this species and the genetic basis underlying the determination of migration direction need further attention, as well as experimental studies of effects of intermediate displacements across longitudes in songbirds and other animals. Therefore, studies of the orientation of more hybrid individuals in this and other migratory divides will be crucial for a broader understanding the mechanisms of selection on this important behavioural trait.

Acknowledgements

We are grateful to the ringers at Ottenby Bird Observatory, Petra Carlsson, Keith Larson and Max Lundberg for assistance in the field and Nils Müller and Jane Jönsson for their help in the molecular laboratory. We particularly thank the two anonymous reviewers for their valuable comments on the manuscript. The project was financed by a project grants (No. 621-2007-5930, 621-2010-5584) from the Swedish Research Council to SÅ, project grant D002-277 from Bulgarian Science Fund and partly by FP7 Capacities project WETLANET to MI. D.P.L.T. was supported with a grant from the National Science and Engineering Council of Canada (a CGS-D and a Michael Smith Foreign Study Scholarship). This is a report from the Centre for Animal Movement Research (CAnMove) financed by a Linnaeus grant (No. 349-2007-8690) from the Swedish Research Council and Lund University. This is contribution no. 261 from Ottenby Bird Observatory.

References

- Åkesson, S., 1993. Effect of geomagnetic field on orientation of the marsh warbler, *Acrocephalus palustris*, in Sweden and Kenya. *Anim. Behav.* 46, 1157–1167.
- Åkesson, S., 1994. Comparative orientation experiments with different species of passerine long-distance migrants: effect of magnetic field manipulation. *Anim. Behav.* 48, 1379–1393.
- Åkesson, S., 1999. Do passerines captured at an inland ringing site perform reverse migration in autumn? *Ardea* 87, 129–138.
- Åkesson, S., 2003. Avian long-distance navigation: Experiments with migratory birds. In: Berthold, P., Gwinner, E., Sonnenschein, E. (Eds.), *Avian Migration*. Springer-Verlag, New York, pp. 472–491.
- Åkesson, S., Bäckman, J., 1999. Orientation in pied flycatchers: the relative importance of magnetic and visual information at dusk. *Anim. Behav.* 57, 819–828.
- Åkesson, S., Hedenström, A., 2000. Selective flight departure in passerine nocturnal migrants. *Behav. Ecol. Sociobiol.* 47, 140–144.

- Åkesson, S., Karlsson, L., Walinder, G., Alerstam, T., 1996. Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in south Scandinavia. *Behav. Ecol. Sociobiol.* 38, 293–302.
- Åkesson, S., Walinder, G., Karlsson, L., Ehnbo, S., 2001. Reed warbler orientation: initiation of nocturnal migratory flights in relation to visibility of celestial cues at dusk. *Anim. Behav.* 61, 181–189.
- Åkesson, S., Walinder, G., Karlsson, L., Ehnbo, S., 2002. Nocturnal migratory flight initiation in reed warblers *Acrocephalus scirpaceus*: effect of wind on orientation and timing of migration. *J. Avian Biol.* 33, 349–357.
- Åkesson, S., Morin, J., Muheim, R., Ottosson, U., 2005. Dramatic orientation shift of white-crowned sparrows displaced across longitudes in the high arctic. *Curr. Biol.* 15, 1591–1597.
- Alerstam, T., Pettersson, S.-G., 1977. Why do migrating birds fly along coastlines? *J. Theor. Biol.* 65, 699–712.
- Bäckman, J., Pettersson, J., Sandberg, R., 1997. The influence of fat stores on magnetic orientation in day-migrating Chaffinch, *Fringilla coelebs*. *Ethology* 103, 247–256.
- Batschelet, E., 1981. *Circular Statistics in Biology*. Academic Press, London.
- Bensch, S., Andersson, T., Åkesson, S., 1999. Morphological and molecular variation across a migratory divide in willow warblers *Phylloscopus trochilus*. *Evolution* 53, 1925–1935.
- Bensch, S., Åkesson, S., Irwin, D.E., 2002. The use of AFLP to find an informative SNP: genetic differences across a migratory divide in willow warblers. *Mol. Ecol.* 11, 2359–2366.
- Bensch, S., Bengtsson, G., Åkesson, S., 2006a. Patterns of stable isotope signatures in willow warbler *Phylloscopus trochilus* feathers collected in Africa. *J. Avian Biol.* 37, 323–330.
- Bensch, S., Irwin, D.E., Irwin, J.H., Kvist, L., Åkesson, S., 2006b. Conflicting patterns of mitochondrial and nuclear DNA diversity in *Phylloscopus* warblers. *Mol. Ecol.* 15, 161–171.
- Bensch, S., Grahn, M., Müller, N., Gay, L., Åkesson, S., 2009. Genetic, morphological, and feather isotope variation of migratory willow warblers show gradual divergence in a ring. *Mol. Ecol.* 18, 3087–3096.
- Berthold, P., 1996. *Control of Bird Migration*. Chapman & Hall, London.
- Berthold, P., Helbig, A.J., Mohr, G., Querner, U., 1992. Rapid microevolution of migratory behaviour in a wild bird species. *Nature* 360, 668–670.
- Biebach, H., Biebach, I., Friedrich, W., Heine, G., Partecke, J., Schmidl, D., 2000. Strategies of passerine migration across the Mediterranean Sea and the Sahara desert: a radar study. *Ibis* 142, 623–634.
- Boles, L.C., Lohmann, K.J., 2003. True navigation and magnetic maps in spiny lobsters. *Nature* 421, 60–63.
- Bruderer, B., Jenni, L., 1990. Migration across the Alps. In: Gwinner, E. (Ed.), *Bird Migration*. Springer, Berlin, pp. 60–77.
- Bruderer, B., Liechti, F., 1998. Flight behaviour of nocturnally migrating birds in coastal areas – crossing or coasting. *J. Avian Biol.* 29, 499–507.
- Buerkle, C.A., 1999. The historical pattern of gene flow among migratory and nonmigratory populations of Prairie Warblers (Aves: Parulinae). *Evolution* 53, 1915–1924.
- Chamberlain, C.P., Bensch, S., Feng, X., Åkesson, S., Andersson, T., 2000. Stable isotopes examined across a migratory divide in Scandinavian willow warblers (*Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula*) reflect their African winter quarters. *Proc. R. Soc. B* 267, 43–48.
- Deutschlander, M., Muheim, R., 2009. Fuel reserves affect migratory orientation of thrushes and sparrows both before and after crossing an ecological barrier near their breeding grounds. *J. Avian Biol.* 40, 85–89.
- Emlen, S.T., Emlen, J.T., 1966. A technique of recording migratory orientation of captive birds. *Auk* 83, 361–367.
- Fischer, J.H., Freake, M.J., Phillips, J.B., 2001. Evidence for the use of magnetic map information by an amphibian. *Anim. Behav.* 62, 1–10.
- Fransson, T., Hall-Karlsson, S., 2008. *Swedish Bird Ringing Atlas Volume 3. Passerines*. Stockholm.
- Freake, M.J., Muheim, R., Phillips, J.B., 2006. Magnetic maps in animals: a theory comes of age? *Q. Rev. Biol.* 81, 327–347.
- Hedenström, A., Pettersson, J., 1984. The migration of Willow Warbler, *Phylloscopus trochilus*, at Ottenby. *Vfu Fågelvård* 43, 217–228 (in Swedish with English summary).
- Hedenström, A., Pettersson, J., 1987. Migration routes and wintering areas of willow warblers *Phylloscopus trochilus* (L.) ringed in Fennoscandia. *Ornis Fennica* 64, 137–143.
- Helbig, A.J., 1991. SE- and SW-migrating Blackcap (*Sylvia atricapilla*) populations in Central Europe: orientation of birds in the contact zone. *J. Evol. Biol.* 4, 657–670.
- Helbig, A.J., 1994. Genetic basis and evolutionary change of migratory directions in a European passerine migrant *Sylvia atricapilla*. *Ostrich* 65, 151–159.
- Helbig, A.J., 1996. Genetic basis, mode of inheritance and evolutionary changes of migratory directions in palaeartic warblers (Aves: Sylviidae). *J. Exp. Biol.* 199, 49–55.
- Helbig, A.J., 2003. Evolution of bird migration: a phylogenetic and bio-geographic perspective. In: Berthold, P., Gwinner, E., Sonnenschein, E. (Eds.), *Avian Migration*. Springer, Berlin, pp. 3–20.
- Irwin, D.E., Irwin, J.H., 2005. Siberian migratory divides: the role of seasonal migration in speciation. In: Greenberg, R., Marra, P.P. (Eds.), *Birds of Two Worlds: The Ecology and Evolution of Migration*. Johns Hopkins University Press, Baltimore and London, pp. 27–40.
- Kiepenheuer, J., 1978. Inversion of the magnetic field during transport: its influence on the homing behaviour of pigeons. In: Schmidt-Koenig, K., Keeton, W.T. (Eds.), *Animal migration, navigation and homing*. Springer-Verlag, Heidelberg, Berlin, pp. 135–142.
- Lundberg, M., Åkesson, S., Bensch, S., 2011. Characterization of a divergent chromosomal region in the willow warbler *Phylloscopus trochilus* using avian genomic resources. *J. Evol. Biol.* 24, 1241–1253.
- Luschi, P., Del Seppia, C., Crosio, E., Papi, F., 1996. Evidence against reliance on magnetic information picked up en route to release sites. *Proc. R. Soc. B* 263, 1219–1224.
- Marchetti, C., Bezzi, E.M., Baldaccini, N.E., 1998. Orientation in relation to exposure to the setting sun in some passerine trans-saharan migrants. *Ethol. Ecol. Evolution* 10, 143–157.
- Marchetti, C., Zehntindjiev, P., 2009. Migratory orientation of sedge warblers (*Acrocephalus schoenobaenus*) in relation to eating and exploratory behaviour. *Behav. Process.* 82, 293–300.
- Moore, F.R., 1986. Sunrise, skylight polarization, and the early morning orientation of night-migrating warblers. *Condor* 88, 493–498.
- Moore, F.R., 1987. Sunset and the orientation behaviour of migrating birds. *Biol. Rev.* 62, 65–86.
- Mouritsen, H., 1998. Redstarts, *Phoenicurus phoenicurus*, can orient in a true-zero magnetic field. *Anim. Behav.* 55, 1311–1324.
- Muheim, R., Moore, F.R., Phillips, J.B., 2006a. Calibration of magnetic and celestial compass cues in migratory birds – a review of cue-conflict experiments. *J. Exp. Biol.* 209, 2–17.
- Muheim, R., Phillips, J.B., Åkesson, S., 2006. Polarized light cues underlie compass calibration in migratory songbirds. *Science* 313, 837–839.
- Nievergelt, F., Liechti, F., Bruderer, B., 1999. Migratory directions of free-flying birds versus orientation in registration cages. *J. Exp. Biol.* 202, 2225–2231.
- Pettersson, J., Hasselquist, D., 1985. Fat deposition and migration capacity of robins *Erithacus rubecula* and goldcrests *Regulus regulus* at Ottenby Sweden. *Ring. Migr.* 6, 66–76.
- Phillips, J.B., 1996. Magnetic navigation. *J. Theor. Biol.* 180, 309–319.
- Phillips, J.B., Adler, K., Borland, S.C., 1995. True navigation by an amphibian. *Anim. Behav.* 50, 855–858.
- Procházka, P., Hobson, K., Karcza, Z., Kralj, J., 2008. Birds of a feather winter together: migratory connectivity in the Reed Warbler *Acrocephalus scirpaceus*. *J. Ornithol.* 149, 141–150.
- Rabøl, J., 1970. Displacement and phaseshift experiments with night-migrating passerines. *Ornis Scand.* 1, 27–43.
- Rabøl, J., 1978. One-direction orientation versus goal area navigation in migratory birds. *Oikos* 30, 216–223.
- Rabøl, J., 1981. Orientation of robins *Erithacus rubecula* after displacement from Denmark to Canary Islands, autumn 1978. *Ornis Scand.* 12, 89–98.
- Richardson, W.J., 1978. Timing and amount of bird migration in relation to weather: a review. *Oikos* 30, 224–272.
- Ruegg, K.C., Smith, T.B., 2002. Not as the crow flies: a historical explanation for circuitous migration in Swainson's thrush (*Catharus ustulatus*). *Proc. R. Soc. B* 269, 1375–1381.
- Sambrook, J., Fritsch, E.F., Maniatis, T., 1989. *Molecular Cloning: A Laboratory Manual*. Cold Spring Harbor Laboratory, Cold Spring Harbor, New York.
- Sandberg, R., 1991. Sunset orientation of robins, *Erithacus rubecula*, with different fields of sky vision. *Behav. Ecol. Sociobiol.* 28, 77–83.
- Sandberg, R., 2003. Stored fat and the migratory orientation of birds. In: Berthold, P., Gwinner, E., Sonnenschein, E. (Eds.), *Avian Migration*. Springer Verlag, Berlin, Heidelberg/New York, pp. 515–525.
- Sandberg, R., Moore, F.R., 1996. Migratory orientation of red-eyed vireos, *Vireo olivaceus*, in relation to energetic condition and ecological context. *Behav. Ecol. Sociobiol.* 39, 1–10.
- Sandberg, R., Moore, F.R., Bäckman, J., Löhmus, M., 2002. Orientation of nocturnally migrating Swainson's thrush at dawn and dusk: importance of energetic condition and geomagnetic cues. *Auk* 119, 201–209.
- Schmaljohann, H., Naef-Daenzer, B., 2011. Body condition and wind support initiate the shift of migratory direction and timing of nocturnal departure in a songbird. *J. Anim. Ecol.* 80, 1115–1122.
- Siegel, S., Castellan, J.N., 1988. *Nonparametric Statistics for the Behavioral Sciences*, 2nd ed. McGraw-Hill International Editions, Blacklick.
- Svensson, L., 1992. *Identification Guide to European Passerines*, 4th ed. British Trust for Ornithology, Stockholm.
- Thorup, K., Rabøl, J., 2007. Compensatory behaviour after displacement in migratory birds. A meta-analysis of cage experiments. *Behav. Ecol. Sociobiol.* 61, 825–841.
- Thorup, K., Bisson, I., Bowlin, M.S., Holland, R.A., Wingfield, J.C., Ramenofsky, M., Wikelski, M., 2007. Evidence for a navigational map stretching across the continental U.S. in a migratory songbird. *Proc. Natl. Acad. Sci. U.S.A.* 104, 18115–18119.
- Thorup, K., Ortvad, T.E., Rabøl, J., Holland, R.A., Tøttrup, A.P., Wikelski, M., 2011. Juvenile songbirds compensate for displacement to oceanic islands during autumn migration. *PLoS ONE* 6 (3), e17903.
- Wiltschko, R., Wiltschko, W., 1995. *Magnetic Orientation in Animals*. Springer, Berlin.
- Wiltschko, W., Wiltschko, R., 1972. Magnetic compass of European robins. *Science* 176, 62–64.

- Wiltschko, W., Wiltschko, R., 1981. Disorientation of inexperienced young pigeons after transportation in total darkness. *Nature* 291, 433–434.
- Wu, L.Q., Dickman, D.J., 2012. Neural correlates of a magnetic sense. *Science* 336, 1054–1057.
- Zar, J.H., 1999. *Biostatistical Analysis*. Prentice Hall, New Jersey.
- Zehnder, S., Åkesson, S., Liechti, F., Bruderer, B., 2002. Observation of free-flying nocturnal migrants at Falsterbo: occurrence of reverse flight directions in autumn. *Avian Sci.* 2, 103–113.
- Zink, G., 1973. *Der Zug europäischer Singvögel. Ein Atlas der Wiederfunde beringter Vögel, vol. 1 Lieferung*. Vogelzug-Verlag, Möggingen.