



Magnetic compass orientation research with migratory songbirds at Stensoffa Ecological Field Station in southern Sweden: why is it so difficult to obtain seasonally appropriate orientation?

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More than three decades ago, Thomas Alerstam initiated the study of orientation and navigation of migratory songbirds in southern Sweden. Stensoffa Ecological Field Station, located approx. 20 km east of Lund, has since been a primary location for orientation experiments. However, it has often been difficult to record well-oriented behaviour in the seasonal appropriate migratory directions, in particular in magnetic orientation experiments under simulated overcast or indoors. Here, we summarise all available experiments testing magnetic compass orientation in migratory songbirds in southern Sweden, and review possible explanations for the poor magnetic compass orientation found in many studies. Most of the factors proposed can be essentially excluded, such as difficulties to extract magnetic compass information at high latitudes, methodological or experimenter biases, holding duration and repeated testing of individual birds, effects of magnetic anomalies and temporal variations of the ambient magnetic field, as well as anthropogenic electromagnetic disturbances. Possibly, the geographic location of southern Sweden where many birds captured and/or tested at coastal sites are confronted with the sea, might explain some of the variation that we see in the orientation behaviour of birds. Still, further investigations are needed to conclusively identify the factors responsible for why birds are not better oriented in the seasonal appropriate migratory direction at Stensoffa.

Migratory orientation and navigation in songbirds has been studied for more than three decades (1982–present) at Lund Univ. in southern Sweden. The main objectives of past and present research are to understand in more detail how migratory birds use directional cues from the Earth's magnetic field, the sun and stars for orientation and navigation. With the study on the role of the geomagnetic field in the development of compass senses in songbirds by Thomas Alerstam and Göran Högstedt (Alerstam and Högstedt 1983), a strong research tradition in orientation and navigation experimentation was initiated at Lund Univ. Since then, Stensoffa Ecological Field Station (hereafter Stensoffa; Fig. 1) has been a primary location for orientation experiments in southern Sweden. Stensoffa has been operated by the Dept of Biology (former Dept of Animal Ecology) at Lund Univ. since the 1960s, and is located in southernmost Sweden, about 20 km east of Lund, in the military training area Revingehed near Lake Krankesjön (Fig. 1). The area surrounding Stensoffa is almost entirely unexploited, with very few private houses. Due to its rural location, the absence of virtually any man-made disturbances, like sound or light pollution, and no measurable electromagnetic disturbances (see below), the field station is an ideal place to carry out orientation experiments with migratory songbirds.

Much effort has been made by different scientists to specifically study magnetic compass orientation at Stensoffa (for references see Table 1–3). However, despite the many orientation studies with migratory songbirds, it has always been somewhat difficult to record well-oriented behaviour in the seasonal appropriate migratory direction in experiments conducted at Stensoffa, compared to other localities (e.g. in Frankfurt, Germany, and in North America; see references below), particularly in indoor experiments testing magnetic compass orientation with restricted visual information. Birds tested at Stensoffa have often been either disoriented or oriented towards directions not corresponding with the seasonally expected migration route (Table 1–3). Here, we review possible causes for the difficulty to demonstrate magnetic compass orientation in migratory songbirds at Stensoffa. We discuss potential effects of different capture and experimental sites, the difficulty to extract magnetic compass information at high latitudes, potential methodological or experimenter biases, the influence of holding duration and repeated testing of individual birds, and extrinsic factors that may pose orientation problems, like magnetic anomalies, temporal variations of the ambient magnetic field and anthropogenic electromagnetic disturbances. We focus on experiments performed indoors or under complete natural or simulated overcast (translucent sheet of Plexiglas placed

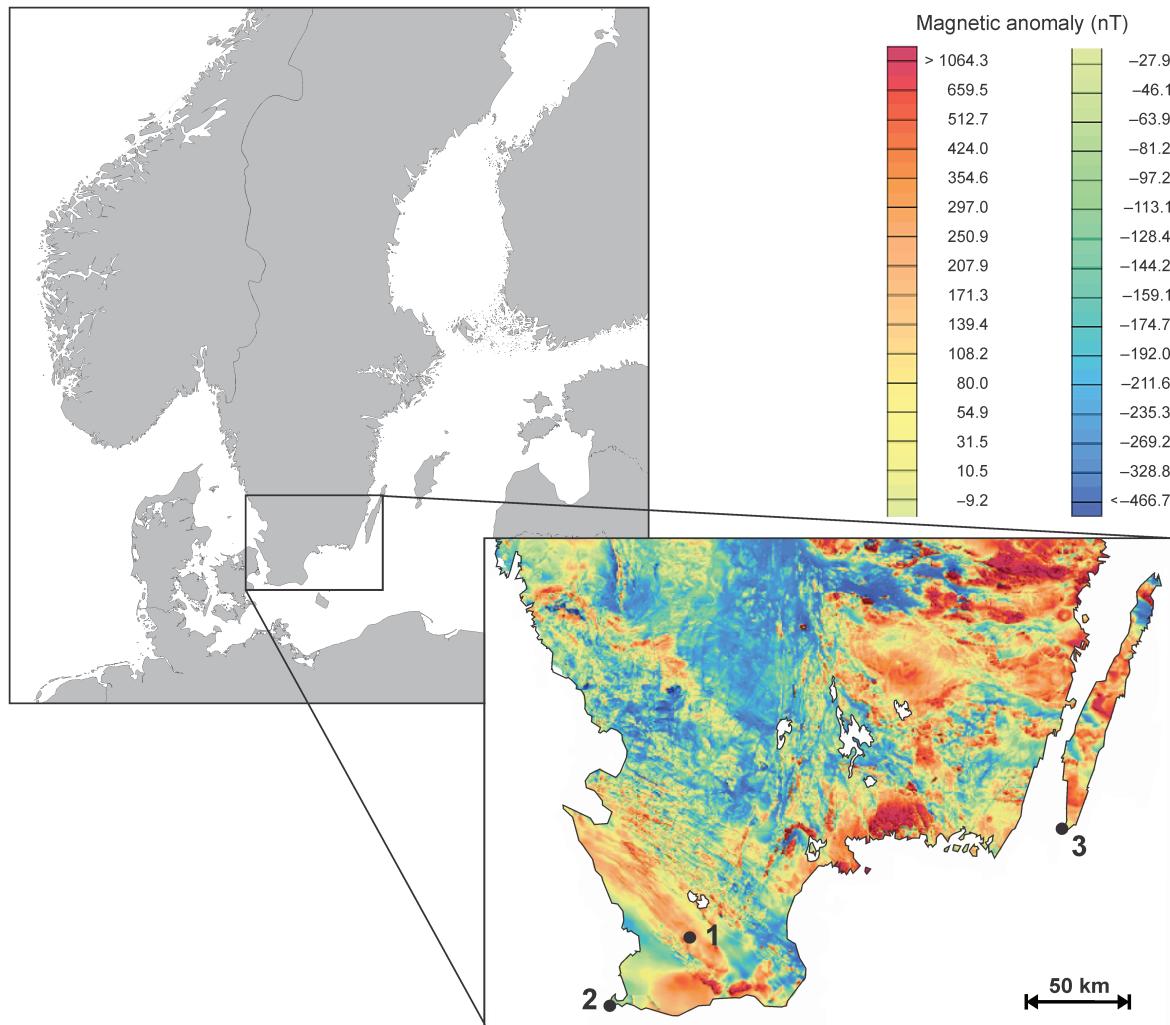


Figure 1. Map of Scandinavia, with inset of southern Sweden showing the locations of 1) Stensöffa Ecological Field Station (55°42'N, 13°27'E), 2) Falsterbo Bird Observatory (55°23'N, 12°49'E), and 3) Ottenby Bird Observatory (56°12'N, 16°24'E). The map in the inset shows magnetic field data of magnetic anomalies of southern Sweden (©Geological Survey of Sweden, SGU). The values give the deviations (in nT) from the reference field DGRF 1965, measured in aerial surveys at 30–60 m elevation above ground between 1960 and 2014.

on top of the orientation cage), in which the problem of recording directed compass orientation is most pronounced, and where the problem of phototactic responses is least pronounced. In orientation experiments carried out at Stensöffa outdoors under clear skies, we have often observed that the birds partly or fully orient towards the brightest part of the sky (Sandberg et al. 1988, Åkesson 1994, Åkesson and Sandberg 1994, Ilieva et al. 2012), which makes it difficult to distinguish whether the birds showed migratory orientation or phototactic responses.

The aim of this review is to discuss the various factors that may explain why it is difficult to record seasonal appropriate migratory orientation in magnetic orientation experiments at Stensöffa in view of the current knowledge on migratory orientation in general and magnetoreception mechanisms in particular. Thereby, we hope to aid other scientists with similar problems to troubleshoot potential problems at their study sites and hopefully improve or better understand the magnetic compass orientation in their study birds.

Effects of capture and experimental sites

The majority of birds used in orientation studies at Stensöffa was either captured in the immediate vicinity of Stensöffa or at one of the nearby bird observatories, Falsterbo Bird Observatory on the southernmost tip of Scandinavia (61 km or ca 55 min by car from Stensöffa), or Ottenby Bird Observatory at the southern point of the island of Öland (332 km or ca 4 h 20 min by car from Stensöffa; Fig. 1; see all available magnetic compass orientation experiments carried out in southern Sweden listed in Table 1–3). Capture site and the migratory disposition of the birds have repeatedly been named to possibly influence the outcome of orientation experiments performed in southern Sweden (Sandberg et al. 1988, Åkesson et al. 1992). Both Falsterbo and Ottenby are typical stopover sites adjacent to larger water bodies, which are believed to force inexperienced, young birds and birds with insufficient energy stores to land (Alerstam 1978, Ralph 1978, Ehnborn et al. 1993, Payevsky 1998). Stensöffa, on the other hand, is located inland (ca 30 km from the nearest

Table 1. Magnetic compass orientation experiments with migratory songbirds carried out outdoors under natural or simulated overcast in southern Sweden. For each experimental group, bird species, age of birds (juv = first year, hatch-year birds; 2y = second-year, after-hatch-year birds; ad = adult birds), testing season, and capture and experimental sites (FBO = Falsterbo, OTT = Ottenby, STS = Sten-soffa) are given (see Fig. 1 for locations). Orientation results are categorized in seasonal orientation along the migration route (experimental groups significantly oriented along the migratory direction according to the Rayleigh test ($p < 0.05$; Batschelet 1981), bimodal seasonal orientation along the migration route (bimodally significant orientation along the migratory direction $\pm 180^\circ$), reverse orientation back along migration route (significant orientation in a direction opposite to the migration direction), orientation perpendicular to migration direction (E-W; significant, unimodal or bimodal orientation in a direction within the interval $90^\circ \pm 25^\circ$ or $270^\circ \pm 25^\circ$), and disorientation (experimental groups not significantly oriented according to the Rayleigh test, $p > 0.05$). Orientation statistics give for each experimental group the unimodal or bimodal mean direction (Dir) relative to magnetic North, the mean vector length (r), the significance value of Rayleigh test (P), and the sample size (n). Groups were considered bimodally oriented when the axial mean vector length was larger than the unimodal vector length. For unpublished data we give the authors and the year of testing as reference. Individual directions were included of those birds that were active (> 40 registrations) and directed (individual mean vector length > 0.05). Individuals were considered as axially oriented when the axial mean vector length was larger than the unimodal vector length. In this case, the side of the axis closer to the unimodal distribution was included in further analyses.

Species	Age	Season	Capture site	Exp. site	Orientation	Dir (°)	r	p	n	Reference
European robin	2y + ad	spring	FBO	STS	disori.	26	0.230	0.114	41	Sandberg et al. 1988
European robin	2y + ad	spring	OTT	OTT	bimodal	36–216	0.420	0.015	24	Sandberg et al. 1988
European robin	juv + ad	autumn	FBO	STS	reverse	332	0.340	0.007	43	Sandberg et al. 1988
European robin	juv + ad	autumn	OTT	OTT	seasonal	174	0.370	< 0.001	89	Sandberg et al. 1988
Northern wheatear	juv	autumn	FBO/OTT	STS/OTT	reverse	331	0.320	0.046	30	Sandberg et al. 1991
European robin	juv + ad	autumn	FBO	FBO	disori.	25	0.060	0.875	37	Ehnbom et al. 1993
European robin	juv + ad	autumn	Uråsa ¹	Uråsa	disori.	201	0.330	0.066	25	Ehnbom et al. 1993
Marsh warbler <i>Acrocephalus palustris</i>	juv	autumn	FBO/Sote Mosse ²	STS	disori.	118	0.190	0.406	25	Åkesson 1993, 1994
Common redstart	2y + ad	spring	FBO	STS	seasonal	25	0.370	0.013	32	Åkesson 1994
Pied flycatcher	2y + ad	spring	FBO	STS	seasonal	14	0.740	0.002	11	Åkesson 1994
Thrush nightingale	2y + ad	spring	FBO/OTT	STS	disori.	92	0.210	0.115	49	Åkesson 1994
Common redstart	juv	autumn	FBO/OTT	STS	disori.	13	0.210	0.347	24	Åkesson 1994
Pied flycatcher	juv	autumn	FBO	STS	E-W	295	0.280	0.043	40	Åkesson 1994
Snow bunting <i>Plectrophenax nivalis</i>	?	spring	OTT	OTT	reverse	226	0.520	0.013	16	Sandberg and Pettersson 1996
Snow bunting	?	autumn	OTT	OTT	reverse	13	0.500	< 0.001	35	Sandberg and Pettersson 1996
Chaffinch <i>Fringilla coelebs</i>	?	autumn	OTT	OTT	disori.	34–214	0.420	0.059	16	Bäckman et al. 1997
Pied flycatcher	juv	autumn	FBO	STS	disori.	293	0.250	0.082	40	Åkesson and Bäckman 1999
Lesser whitethroat	2y + ad	spring	FBO	FBO	disori.	289	0.252	0.088	38	Muheim (unpubl. [2001, 2002])
European robin	2y	spring	FBO	FBO	reverse	175	0.474	0.040	14	Muheim (unpubl. [2001, 2002])
European robin	ad	spring	FBO	FBO	disori.	271–91	0.410	0.056	17	Muheim (unpubl. [2001, 2002])
Willow warbler	juv (few ad)	autumn	OTT	OTT	disori.	152–332	0.150	0.521	29	Ilieva et al. 2012
Willow warbler	juv (few ad)	autumn	OTT	STS	disori.	141–321	0.210	0.291	28	Ilieva et al. 2012
Willow warbler	juv (few ad)	autumn	STS	STS	disori.	14	0.210	0.266	30	Ilieva et al. 2012
Willow warbler	juv (few ad)	autumn	STS	STS	disori.	263	0.310	0.090	25	Ilieva et al. 2012
Willow warbler	juv (few ad)	autumn	STS	OTT	disori.	220–40	0.370	0.065	20	Ilieva et al. 2012
European robin	juv	autumn	STS	STS	seasonal	167	0.550	< 0.001	41	Åkesson et al. 2015
Sedge warbler <i>Acrocephalus schoenobaenus</i>	juv	autumn	STS	STS	disori.	170	0.310	0.215	16	Åkesson et al. 2015
Duncock	juv	autumn	STS	STS	seasonal	175	0.290	0.008	58	Åkesson et al. 2015

¹ 56°41'N, 14°53'E.

² 55°25'N, 13°25'E.

Table 2. Magnetic compass orientation experiments with migratory songbirds carried out indoors at Stensoffa under low-irradiance (1–3 mW m⁻²), full-spectrum or green (521 or 560 nm) light conditions, known to typically lead to oriented behaviour towards the seasonally appropriate migratory direction (cf. Wiltschko et al. 2001, 2002, Muheim et al. 2002). See Table 1 for further explanation.

Species	Age	Season	Capture site	Exp. site	Orientation	Dir (°)	r	p	n	Reference
Lesser whitethroat	juv	autumn	OTT	STS	disori.	346–166	0.203	0.331	27	Muheim (unpubl. [2000])
Lesser whitethroat	juv	autumn	OTT	STS	disori.	57–237	0.181	0.525	16	Muheim (unpubl. [2001])
European robin	juv	autumn	OTT	STS	seasonal	215	0.491	0.005	21	Muheim et al. 2002
European robin	juv	autumn	OTT	STS	disori.	244–64	0.130	0.738	19	Muheim et al. 2002
Lesser whitethroat	juv	autumn	OTT	STS	disori.	185	0.246	0.222	25	Muheim (unpubl. [2002])
Lesser whitethroat	juv	autumn	OTT	STS	disori.	259	0.243	0.229	25	Muheim (unpubl. [2002])
Lesser whitethroat	juv	autumn	OTT	STS	disori.	248–68	0.226	0.330	22	Muheim (unpubl. [2002])
Lesser whitethroat	2y	spring	FBO	STS	disori.	194	0.430	0.088	13	Muheim, Sjöberg, Pfuhl (unpubl. [2011])

coast to the south), thus the birds caught there are either transients or are stopping over in seemingly suitable habitat (forest, swamp or reed beds; Fig. 1).

In a study carried out in the 1980s, Roland Sandberg, Jan Pettersson and Thomas Alerstam found some interesting differences in magnetic compass orientation between European robins *Erithacus rubecula* captured and tested for orientation at Ottenby and robins captured in Falsterbo and transported to Stensoffa for testing (Sandberg et al. 1988). Robins captured and tested during spring or autumn migration at Ottenby were well oriented towards the seasonal appropriate migratory directions, whereas birds captured in Falsterbo and tested at Stensoffa were disoriented during spring migration and showed reverse orientation back along the migration route during autumn migration (Sandberg et al. 1988).

To assess whether there were differences in magnetic compass orientation between birds captured and/or tested at Stensoffa, Falsterbo or Ottenby, respectively, we compared the results of the available orientation experiments from these three sites (Table 4). We defined experimental groups as ‘oriented towards the expected direction’, if the group was significantly oriented according to the Rayleigh test ($p < 0.05$; Batschelet 1981) and if the orientation was directed in seasonally appropriate migratory directions (northerly directions [$0^\circ \pm 65^\circ$ relative to magnetic north] during spring and southerly directions [$180^\circ \pm 65^\circ$] during autumn), or if the orientation was bimodally directed along the migration route (see Table 1 for details). Interestingly, we found striking differences between the magnetic compass orientation of short- and long-distance migrants at the different sites. Both groups of short-distance migrants, in this case European robins, captured and tested at Ottenby were oriented towards the expected direction (Table 4). The three groups of robins captured and tested at Falsterbo were either disoriented ($n = 2$) or showed reverse orientation ($n = 1$; see Table 1 for definition of reverse orientation). Short-distance migrants (European robins and dunnocks *Prunella modularis*) captured and tested at Stensoffa were oriented towards the expected migratory direction in 67% of all experiments ($n = 3$; Table 4). Of the six groups of robins captured at Ottenby and tested at Stensoffa, only 50% showed orientation along or bimodally along the migratory route, while none of the five groups caught at Falsterbo and tested at Stensoffa was oriented towards the expected direction. These results suggest that robins from Falsterbo were generally poorly oriented, while birds captured at Ottenby or Stensoffa oriented towards the expected directions to a higher degree.

Reasons for the observed differences in orientation between sites have been discussed in detail by Sandberg et al. (1988) and Åkesson et al. (1992). It has been pointed out that the discrepancies between sites may reflect different bird populations in different stages of their migration moving through Ottenby and Falsterbo, respectively. A large proportion of the birds migrating through Ottenby during autumn might have crossed the Baltic Sea before reaching Öland (Pettersson and Lindholm 1983, Pettersson et al. 1990). Birds caught during autumn migration at Falsterbo, and possibly also at Stensoffa, on the other hand, might have migrated mostly overland (Karlsson et al. 1988, Åkesson et al. 1992). However, we currently know too little about the migratory routes of different bird populations migrating through Ottenby and Falsterbo to draw any firm conclusions.

A possible explanation for the differences between robins captured and tested at Ottenby compared to robins captured at Ottenby and tested at Stensoffa could be that the car transport negatively affected the birds, as has been described in homing pigeons (Del Seppia et al. 1996). However, the percentage of experimental groups that were oriented in the expected direction did not differ between groups transported between capture and experimental site (23% of 22 groups) and groups experiencing no transport (31%; $n = 13$), which does not suggest an effect of transportation on the birds’ orientation performance. Also, the effect of transport on orientation has been tested in a recent study with willow warblers *Phylloscopus trochilus* that were either caught at Ottenby or Stensoffa and tested at the capture site or transported to the other site and tested there (Ilieva et al. 2012). The only group of birds that showed near-significant orientation ($p = 0.065$) towards the expected direction (though bimodal) was the group of willow warblers captured at Stensoffa and tested at Ottenby, making an effect of transport rather unlikely.

Magnetic compass orientation of long-distance migrants captured and tested at the different sites suggests a different pattern from that of the short-distance migrants. While short-distance migrants oriented in 37% of all experiments towards the expected direction, long-distance migrants did so in only 12.5% of experiments ($n = 19$ and $n = 16$ experimental groups, respectively; Table 4). None of the groups of long-distance migrants captured at Ottenby was oriented, irrespective of testing site (0%; $n = 7$), and the same was true for birds captured and tested at Stensoffa (0%; $n = 3$). However, two of the five groups (40%) of long-distance migrants captured at Falsterbo and tested at Stensoffa were oriented

Table 3. Magnetic compass orientation experiments with migratory songbirds carried out indoors at Stensoffa under low-irradiance (1–3 mW m⁻¹), full-spectrum (in year 2002) or green (521 or 560 nm; all other years) light conditions. Individual birds were repeatedly tested under the same experimental condition. For each experimental group, the orientation based on the first experiment of each individual bird is shown in the upper row (number of experiments per bird = 1), and the mean orientation based on the individual mean orientation from the repeated experiments of each individual bird is given in the lower row (number of experiments per bird ≥ 3). As a measure of how consistently the individual birds were oriented between the repeated experiments, we give the mean of the individual mean vector lengths and the standard deviation (ind. $r \pm$ STD). See Table 1 for further explanation.

Species	Age	Season	Capture site	Exp. site	Orientation	Dir (°)	r	p	n	Exp./bird	Individual $r \pm$ STD	Reference
E. robin	juv	autumn	OTT	STS	disori.	357–177	0.113	0.761	22	1		Muheim (unpubl. [2002])
					seasonal	129	0.399	0.028	22	3–5	0.592 \pm 0.158	
E. robin	2y	spring ¹	OTT	STS	disori.	163	0.334	0.170	16	1		Muheim (unpubl. [2003])
					bimodal	154–334	0.464	0.029	16	3–4	0.780 \pm 0.159	
E. robin	juv	autumn	OTT	STS	disori.	55	0.230	0.149	36	1		Muheim (unpubl. [2003])
					reverse	62	0.371	0.006	36	3–13	0.362 \pm 0.171	
E. robin	2y	spring ²	OTT	STS	seasonal	39	0.367	0.038	24	1		Muheim (unpubl. [2004])
					E-W	79	0.355	0.047	24	3–8	0.644 \pm 0.150	
E. robin	juv	autumn	FBO	STS	disori.	42–222	0.221	0.465	16	1		Muheim (unpubl. [2009])
					disori.	228	0.174	0.625	16	3–9	0.532 \pm 0.241	
E. robin	juv	autumn	STS	STS	disori.	101–281	0.127	0.685	24	1		Muheim (unpubl. [2009])
					disori.	155	0.296	0.122	24	3–8	0.570 \pm 0.157	
E. robin	2y	spring	FBO	STS	disori.	152	0.130	0.531	38	1		Muheim, Sjöberg, Pühl (unpubl. [2011])
					disori.	95	0.183	0.280	38	3–5	0.717 \pm 0.201	
E. robin	juv + ad	autumn	FBO	STS	disori.	233	0.370	0.084	18	1		Muheim, Sjöberg, Pühl (unpubl. [2011])
					disori.	195–15	0.341	0.123	18	3–5	0.588 \pm 0.197	

¹ birds captured, but not tested, during autumn 2002.

² birds captured and tested during autumn 2003.

towards the expected migratory directions. In both cases, the birds (pied flycatchers *Ficedula hypoleuca* and common redstarts *Phoenicurus phoenicurus*) were tested during spring migration, while comparative experiments during autumn migration led to westerly directions or disorientation (Table 1 and 4). Earlier studies did not find any site-specific differences in the orientation of long-distance migrants. Sandberg et al. (1991) found no significant differences in either the direction or scatter of orientation between Northern wheatears captured and tested at Ottenby and birds captured at Falsterbo and tested at Stensoffa. Also, thrush nightingales *Luscinia luscinia* and common redstarts captured during autumn migration at either Falsterbo or Ottenby and transported to Stensoffa were both disoriented (Åkesson 1994).

It is possible that the confrontation with the sea at the coast might affect the orientation behaviour of the birds captured and/or tested at coastal sites, like Falsterbo and Ottenby. During autumn, many of the individuals will be confronted with their first unavoidable sea crossing on their route south from the Scandinavian peninsula, which might lead to a variety of behavioural responses, like reverse migration in leaner individuals (Åkesson et al. 1996, Nilsson and Sjöberg 2016). In spring, many of the birds may be near the end of their migration, which likely contributes to increased inter-individual variation in orientation directions (Karlsson et al. 2010). Two experimental groups showed bimodal orientation along the migration route, with some individuals orienting towards the seasonally expected migratory direction and some individuals showing reverse orientation, i.e. orientation back along the migration route (Table 1, 3 and 4). Both groups were robins captured during spring migration at Ottenby and tested at either Ottenby or Stensoffa (Table 4). Reverse migration was observed in three groups of robins and a group of northern wheatears *Oenanthe oenanthe* captured at either Falsterbo or Ottenby (Table 4). Ringing recoveries and visual observations of songbirds at Falsterbo show a considerable degree of reverse migration (Sandberg et al. 1988, Åkesson et al. 1996). This is in contrast to birds caught at inland stopover sites, where reverse migration is not expressed to the same degree (Åkesson 1999). However, the number of experimental groups is too small to make any firm conclusions. Taken together, there appears to be no clear pattern in when and under what circumstances the birds fail to orient towards the expected directions, which makes it unlikely to find simple and general explanations at this point.

In comparison to the magnetic compass orientation of birds captured and tested in southern Sweden, birds captured and tested in Frankfurt tend to be more concentrated towards the seasonally expected migratory direction (Wiltshko and Wiltshko 1972, 1995, Wiltshko et al. 2000, 2001). It is interesting to note that the birds, mainly juvenile robins, tested in Frankfurt are probably from the Scandinavian population, since their capture is timed to occur one to two days after mass captures at Falsterbo Bird Observatory (R. and W. Wiltshko pers. comm.). Also, the individuals with longer wings are selected to ensure that the birds come from a Scandinavian population rather than from northern Germany. Thus, robins used in experiments performed in Frankfurt have likely migrated farther than Swedish birds caught at either one of the three captures sites in southern

Table 4. Summary of outcomes of magnetic compass orientation experiments carried out in southern Sweden (Table 1–3). For each subgroup, we give the number of experiments resulting in seasonal orientation along the migration route, bimodal orientation along the migration route, reverse orientation back along the migration route, orientation perpendicular to the migration route, and disorientation (see Table 1 for definitions). The last two columns give the total number of experiments and the percentage of experiments that resulted in seasonal or bimodal seasonal orientation along the migration route. We excluded experimental groups with multiple capture or experimental sites, a study carried out at Uråsa, and three experimental groups with diurnal migrants (chaffinches and snow buntings). For studies presented in Table 3, we used the results from the repeated experiments with individual birds. European robins and dunnocks were defined as short-distance migrants, all other species as long-distance migrants.

	Seasonal orientation along migration route	Bimodal seasonal orientation along migration route	Reverse orientation back along migration route	Orientation perpendicular (E-W) to migration route	Dis-orientation	Total number of experiments	% Orientation (seasonal or bimodal seasonal) along migration route
Capture site – experimental site (short-distance migrants)							
STS-STs	2	0	0	0	1	3	67
OTT-STs	2	1	1	1	1	6	50
FBO-STs	0	0	1	0	4	5	0
OTT-OTT	1	1	0	0	0	2	100
FBO-FBO	0	0	1	0	2	3	0
Capture site – experimental site (long-distance migrants)							
STS-STs	0	0	0	0	3	3	0
OTT-STs	0	0	0	0	6	6	0
FBO-STs	2	0	0	1	2	5	40
OTT-OTT	0	0	0	0	1	1	0
FBO-FBO	0	0	0	0	1	1	0
Transport between capture and experimental site							
yes	4	1	2	2	13	22	23
no	3	1	1	0	8	13	31

Sweden. It is unclear whether migratory experience might play a role, with birds, especially juveniles, orienting more directed towards the end of their migration, compared to the beginning. However, seasonal effects are not visible in North America, where white-throated sparrows *Zonotrichia albicollis* were equally well-oriented in the seasonal appropriate migratory direction during autumn at the beginning of their migration, as during spring when approaching their breeding area (Deutschlander and Muheim 2009, Muheim et al. 2009). Thus, rather than migratory experience, the approach to and confrontation with the sea in southern Sweden, compared to migration mainly over land in continental Europe, could be a possible explanation for the differences between studies carried out in southern Sweden and Frankfurt.

Difficulty to extract magnetic compass information at high latitudes

The higher latitude and corresponding steeper inclination of the Earth's magnetic field lines in southern Sweden (70° inclination) compared to Frankfurt (66° inclination) may pose problems for birds to extract magnetic compass information. Birds have a so-called inclination compass (Wiltschko and Wiltschko 1972), thus they have to identify the north-south axis of the geomagnetic field lines and determine which side of this axis points towards the equator or the closest pole, respectively. It is likely that the steeper the inclination of the magnetic field lines, the more difficult it is to correctly determine the magnetic north-south axis, i.e. the more difficult it becomes to determine the correct migratory direction. However, experiments at locations with equally large magnetic inclinations, like Rybachy (70° inclination), do not report the same problems that we find at Stenoffa (Kavokin et al. 2014). Also, orientation experiments performed at

even higher latitudes than southern Sweden have shown that migrating birds are able to detect magnetic compass information at very steep angles of inclination (as steep as 98°; Sandberg et al. 1991, 1998, Åkesson et al. 1995, 2001, 2005, Gudmundsson and Sandberg 2000, Muheim and Åkesson 2002, Muheim et al. 2006, Lefeldt et al. 2015). Weindler et al. (1995) pointed out that the problem of steep inclination might be more pronounced in hand-raised birds than in wild-caught birds that had access to a variety of other cues (stars, sun, etc.) during ontogeny when the different compasses are learned and calibrated with each other. They found that pied flycatchers that were hand-raised without view of celestial cues in Latvia (73° inclination) oriented bimodally along the migration route, while birds hand-raised under the same conditions in Frankfurt, Germany, oriented unimodally towards the seasonally expected migratory directions (Weindler et al. 1995). However, Sandberg et al. (1991) did not find any difference in orientation under simulated overcast between European wheatears hand-raised and tested at Ottenby and birds captured during the autumn migration season at neither Falsterbo nor Ottenby and tested at Stenoffa or Ottenby. Thus, it is unlikely that steep magnetic field lines associated with high latitudes are the major cause for the poor magnetic orientation performance under overcast observed in south Sweden.

Methodological or experimenter biases

A variety of different methods have been used over the years to measure the orientation responses of migratory birds. Alerstam and Högstedt (1983) visually observed the directional movements of birds in round orientation cages positioned above ground, so that an experimenter could lie underneath the cage, facing the sky, and thereby observe the

bird through the transparent bottom. During later years, this method was replaced by traditional Emlen funnels lined with typewriter correction paper, and in recent years with thermal paper (Emlen and Emlen 1966, Mouritsen et al. 2009) and automatic registration cages. The automatic orientation cages developed at Lund Univ. (by J. Bäckman and G. Göransson) consisted of eight movable sections connected to electronic micro-switches, registering each time a bird pressed down a section (Sandberg et al. 1988). Initially, the micro-switches were connected to counters revealing the total number of registrations at the end or at intermediate intervals of the experiment (Åkesson and Sandberg 1994). In later modifications, the registration system was connected to a computer, allowing time-resolved data registration (Åkesson and Bäckman 1999, Muheim et al. 2002). Most recently, we have started to use video tracking methods to record the orientation movements of passerine migrants (Muheim et al. 2014, Bianco et al. 2016).

The pros and cons of the different shapes and sizes of funnels and cages used in orientation experiments have been extensively discussed (Helbig 1991, Nievergelt and Liechti 2000, Muheim et al. 2014). The orientation funnels used in the majority of our studies were slightly shallower than the original Emlen funnels used in Frankfurt and Australia (Emlen and Emlen 1966, Helbig 1991). In a series of experiments carried out between 2009 and 2011 (Table 2, 3), we tested the magnetic orientation of European robins, and lesser whitethroats *Sylvia curruca* indoors using exact copies of the original Emlen funnels which we had successfully used in experiments at Braddock Bay Bird Observatory, NY, USA (Deutschlander and Muheim 2009, Muheim et al. 2009). However, the orientation of the birds tested with these funnels at Stensoffa was not better directed towards the seasonal appropriate migratory directions than birds tested in the funnels traditionally used at Stensoffa (Table 2 and 3). Thus, funnel shape and size unlikely cause the disorientation of the birds at Stensoffa. It is also worth noting that most of the equipment used to record the orientation of migratory songbirds in southern Sweden has also been used abroad (Alaska, southern United States, northern Canada, Greenland, Kenya, Russia). On average, the birds tested for magnetic compass orientation in studies abroad oriented more concentrated towards the species-specific migratory directions (Åkesson 1994, Sandberg et al. 2000, 2002, Åkesson et al. 2001, 2005, Muheim et al. 2006) than in studies carried out in Sweden, which argues against methodological or experimenter biases.

Effects of holding duration

Time in captivity before the start of the orientation experiments might be an important factor for successful experiments generating orientation towards the seasonal appropriate migratory direction. Testing birds immediately after capture has been shown to lead to phototactic behaviour towards the brightest area in the funnel or the light source itself (sun or moon; Muheim and Jenni 1999, Muheim et al. 1999, Ilieva et al. 2012). Birds tested in Germany and Australia, for example, were usually held for several weeks before the start of the experiments (Wiltschko et al. 1994, Wiltschko and Wiltschko 1995). Keeping the experimental birds in

cages for at least some days before the start of the orientation experiments allows them to get used to captivity and be handled by humans, which in turn is expected to reduce stress. Ample time between capture and the start of the orientation experiments also allows the birds to replenish their fat reserves, which has been shown to be important for seasonal appropriate orientation towards the migratory direction (cf. Sandberg and Moore 1996, Bäckman et al. 1997, Sandberg et al. 2002, Deutschlander and Muheim 2009). In orientation experiments carried out in the early 1980s at Stensoffa, Thomas Alerstam and Göran Högstedt exposed nestling pied flycatchers during June to a shifted magnetic field in their nest boxes and subsequently brought the birds into the lab before they fledged (Alerstam and Högstedt 1983). During August, once the birds had developed migratory restlessness, they were tested for orientation in outdoor cages with access to both magnetic and celestial compass cues. The birds were consistently oriented, at least in the beginning of the migration season, however towards westerly directions (Alerstam and Högstedt 1983), instead of the southwesterly or south-southwesterly directions expected from ringing recoveries (Fransson and Hall-Karlsson 2008). Thus, the long holding duration did not lead to more concentrated orientation towards the seasonal appropriate migratory directions, at least not in this case.

In the majority of experiments carried out at Stensoffa more recently, including all indoor experiments (Table 2 and 3), the birds were kept for several days in captivity before the start of the first orientation experiment. Individual birds were only tested for orientation when fat scores were larger than 2 (according to the visual scale for fat classification from 0–9, based on Pettersson and Hasselquist 1985 and modified for Falsterbo Bird Observatory as given in Sjöberg et al. 2015). These birds also clearly displayed migratory restlessness in their holding cages during the night, so they were in full migratory disposition. Still, in many experiments the birds were not significantly oriented towards the species-specific migratory direction (Table 2 and 3), suggesting that holding duration is not the decisive factor explaining why birds tested at Stensoffa don't perform that well.

Effects of premature initiation of migratory restlessness

The Wiltschko group has been very successful in holding birds for several months and 'advancing' their migratory program to initiate migratory disposition at an earlier date than it would naturally occur (Wiltschko 1968, Wiltschko and Wiltschko 1995, Wiltschko et al. 2000, 2001). They captured their experimental birds during autumn migration, held them over winter and initiated spring migratory restlessness by artificially prolonging day length in the holding room in late winter. They report that these birds were much better motivated to show migratory activity, and oriented towards the species-specific migratory direction much more consistently than birds tested under the normal circannual scheme (Wiltschko and Wiltschko 1995, Wiltschko et al. 2000, 2001, Ritz et al. 2004). We made two attempts to investigate whether long-term holding and premature initiation of migratory restlessness would improve the orientation performance of migratory birds at

Stensoffa. During autumn 2002 and 2003, we caught juvenile European robins during their first autumn migration at Ottenby Bird Observatory and brought them to Stensoffa. Both groups were kept over winter indoors under the light regime of southern Sweden. Following the procedure used by the Wiltschko group (for references, see above), we started to prolong day length in late December to prematurely induce migratory disposition. Once the birds had accumulated subcutaneous fat and started to display nocturnal migratory restlessness in their cages, we tested them for magnetic compass orientation indoors under low-irradiance ($1\text{--}3\text{ mW m}^{-1}$), 560 nm green light for magnetic compass orientation (Fig. 2a, Table 3). We had earlier shown that robins were well oriented under this light condition (Muheim et al. 2002). The experiments took place in the same room used during autumn 2001 (Muheim et al. 2002), with the only difference that the nine orientation cages were placed in the middle of a vertical magnetic coil ($420 \times 420\text{ cm}$; Helmholtz design). Each bird was tested for one hour during four nights in the natural magnetic field in one of the nine randomly chosen funnels. Despite the long-term holding and premature initiation of migratory restlessness, however, the robins oriented axially towards southeast-northwest during spring 2003 (Fig. 2a) and towards easterly directions during spring 2004 (Fig. 2c, Table 3). Some of the individuals from the latter group were also tested during autumn 2003, and chose easterly directions already then (Fig. 2b, Table 3). In fact, the subset of individual birds tested during both autumn 2003 and spring 2004 did not orient significantly different from each other (Watson U^2 -test: $U^2 = 0.154$, $p > 0.05$, $df_1 = 24$, $df_2 = 24$). Thus, long-term holding and prematurely initiating migratory disposition led to significant orientation, but towards unexpected directions.

Repeated testing of individual birds

Repeated testing of individual birds under the same experimental condition has also been argued to provide a better measure of a bird's directional choice, leading to higher concentration of directions, compared to testing birds only once under a condition. Testing individual birds several times under the same condition makes it possible to calculate an individual mean direction for each bird, which reduces some of the variation in the directional choices between tests. The Wiltschko group has successfully used this method. They typically tested each individual bird between three and five times (Wiltschko et al. 2000, 2001, Ritz et al. 2004). Interestingly, their birds usually showed a very high consistency in orientation directions between tests. The individual mean vector lengths, which are a measure of how consistent an individual bird was oriented between experiments, were typically larger than 0.75 on a scale between 0 and 1, with 0 indicating no consistency and 1 showing a high agreement in the directional choices between experiments. In a series of experiments between 2002 and 2011, we repeatedly tested European robins under the same experimental condition in indoor experiments, and compared the orientation based on the first experiment of each individual bird with the orientation based on the repeated experiments (Table 3). We found that the orientation based on the repeated experiments of each individual bird was generally less scattered than the orientation based on the first experiment (Table 3). However, the directional choices of the birds corresponded with the seasonally appropriate migratory orientation only to a limited degree (Fig. 2a, Table 3). Still, the individual birds showed a remarkable consistency in their directional choices, as seen by the relatively long individual mean vector lengths (Table 3), which were however slightly more scattered

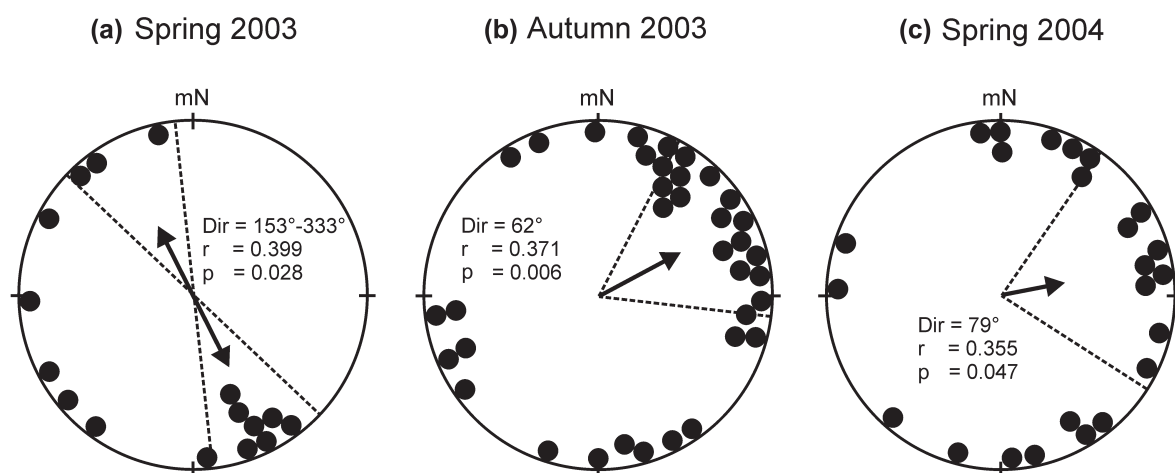


Figure 2. Magnetic compass orientation of European robins caught during their first migration at Ottenby Bird Observatory and tested indoors under low-irradiance ($1\text{--}3\text{ mW m}^{-1}$), 560 nm green light at Stensoffa Ecological Field Station. (a) Orientation of birds captured during autumn 2002 and tested in early spring 2003. (b) Orientation of birds captured and tested during autumn 2003. (c) Orientation of birds captured during autumn 2003 and tested in early spring 2004. Individual mean directions were included for all birds that were active (> 40 registrations) and directed (individual mean vector length > 0.05) in at least three experiments. Birds were considered as axially oriented when the axial mean vector length was larger than the unimodal vector length. In this case, the side of the axis closer to the unimodal distribution was included. Each dot represents the mean orientation of an individual bird tested repeatedly under the same experimental condition. The arrows give the mean direction and the length is proportional to the mean vector length r with the radius of the circle = 1. The double arrow in (a) indicates a bimodally oriented experimental group (axial mean vector length $>$ unimodal vector length). Dotted lines indicate the 95% confidence interval. See Table 3 for details.

than the birds tested in Frankfurt (Wiltshko et al. 2000, 2001, Ritz et al. 2004). It indicates that the individual birds seemed to have been highly motivated to orient towards a specific direction. In two cases, the orientation based on the first experiment of each individual bird was more concentrated than the orientation based on the repeated experiments (spring 2004, autumn 2011), but only the group of birds tested during autumn 2011 was significantly oriented. Thus, repeated testing of birds under an experimental condition reduced the large scatter in the directional choices of the birds in magnetic orientation experiments often observed at Stensoffa to some degree. However, it did not result in more reliable orientation towards the seasonally inappropriate migratory directions.

Magnetic anomalies and temporal variations of the ambient magnetic field

Instabilities of the ambient magnetic field, like permanent magnetic anomalies and temporal variation of the geomagnetic field, must be considered when studying the use of magnetic field cues for orientation and navigation in animals. Depending on the scale of the movements, the orientation system may be sensitive to magnetic anomalies and magnetic field changes to different degrees, i.e. small-scale movements require more accurate information than large-scale movements, and are therefore expected to be also more sensitive to disturbances (Phillips 1996, Freake et al. 2006).

The avian magnetic compass has been shown to function within a narrow window around the natural intensity range of the Earth's magnetic field. Birds tested in artificial magnetic fields with intensities much weaker or much stronger than the Earth's magnetic field became disoriented (Wiltshko 1968, Wiltshko et al. 2006). However, after pre-exposure to such unnatural magnetic fields for as little as a few hours, the birds have been shown to be able to orient under these manipulated conditions (Wiltshko 1978, Wiltshko et al. 2006). Also homing pigeons have been reported to be able to orient when released from magnetic anomalies, if they were able to familiarize themselves with the area before release (Kiepenheuer 1982, 1986, Wagner 1983, Lednor and Walcott 1988). Thus, birds appear to be able to learn or adapt to changing properties of the ambient magnetic field, i.e. they can learn to orient under novel magnetic conditions, or the functional range of their magnetoreceptor is flexible and allows adjustment to previously not experienced magnetic conditions, making it possible for birds to use their magnetic compass, provided that the magnetic field contains directional information.

Geomagnetic field measurements in Sweden show strong, large-scale magnetic anomalies in northern Sweden in the area of Kiruna and central Sweden (Geological Survey of Sweden, SGU). With a tracking radar, Thomas Alerstam studied the behaviour of migrating birds flying over one of these strong magnetic anomalies with up to 60% increase in total intensity compared to normal values (Alerstam 1987). He found no signs of birds avoiding the anomaly and observed only rarely birds that changed direction when they crossed the anomaly. The birds, however, reacted to the anomaly by making abrupt dives, i.e. drops in flight altitude, especially when crossing areas with abnormally steep inclinations and

high intensities (Alerstam 1987). These observations indicate that birds are aware of changing magnetic conditions during migration, and that they are able to react to local variations of the magnetic field by changing their behaviour, but at least in this case, they did not become disoriented.

There are some minor magnetic field anomalies in southern Sweden near Stensoffa, Falsterbo and Ottenby, but they do not exceed ± 250 nT, which is less than 0.5% of the background field (Fig. 1). Extensive magnetic field measurements by us at Stensoffa in both holding and testing facilities and outdoors, however, have not revealed any local gradients and deviations from the magnetic field properties predicted by magnetic field models. If a static magnetic field anomaly was present at Stensoffa, we would predict a systematic change in the birds' magnetic compass orientation, rather than the disorientation and the orientation in various directions that we often observe (Table 1–3). Thus, it is unlikely that magnetic anomalies are the cause for the poor magnetic orientation that we observe in indoor and simulated overcast experiments at Stensoffa.

Daily variations of the geomagnetic field and magnetic storms caused by solar radiation have been shown to influence magnetic orientation of birds, both homing pigeons and migratory passerines. Several studies have reported reduced speed and/or success in homing experiments or races with pigeons performed during or shortly after magnetic storms (Keeton et al. 1974, Schiffner and Wiltshko 2011). The relatively small daily fluctuations of the magnetic field caused by solar activity in the range of 10–30 nT (Tenforde 1995) have in some cases shown to impair the homing abilities of pigeons in a systematic way which suggested that these natural fluctuations might be integrated in their navigation system (Wiltshko et al. 1986, Becker 1991). In homing animals, however, it is more likely that small changes in magnetic field intensity cause misreading of the magnetic map involved in positioning (cf. Phillips 1996, Freake et al. 2006, Phillips et al. 2006). Still, a few early radar and visual observations (ceiometer and moon watching) studies reported that increasing disturbances of the magnetic field affected the orientation of migrating birds (Richardson 1976, Moore 1977). Recently, long-term ringing data of juvenile ruff *Philomachus pugnax* at a migratory stopover indicated a correlation between the year-specific sex ratio and the global magnetic field disturbance, suggesting that males and females might respond differently to geomagnetic disturbance with changes in either the direction of migration or the level of migratory activity (Rakhimberdiev et al. 2014).

Solar activity peaks in approx. 11-yr cycles, with recent peaks in 1989–1992, 2000–2002, 2012–2014 (Pesnell 2015), which potentially could have interfered with some of our most experiments. However, there is no obvious pattern visible in the available data (Table 1–3). Also, magnetic storms are a global phenomenon, although considerably reduced at the sun-averse side of the Earth (during local nights), thus other orientation experiments carried out at other places on the globe should have been impaired to the same degree. There is no indication of this, especially not from Frankfurt (Wiltshko et al. 1994, 2000, 2001, Wiltshko and Wiltshko 1995, Ritz et al. 2004), which lies at about the same longitude as southern Sweden and should

have been exposed to similar magnetic disturbances during the past years. We consider it unlikely that daily variations of the magnetic field, including magnetic storms, are causing the poor magnetic orientation performance of the birds tested at Stensoffa.

Anthropogenic electromagnetic disturbances

Weak, radio-frequency electromagnetic fields ('RF-fields') in the lower MHz range (1–10 MHz) have been shown to disrupt magnetic compass orientation of birds and other animals by directly interfering with the primary magnetoreception process of the light-dependent magnetic compass (Ritz et al. 2004, 2009, Engels et al. 2014, Muheim et al. 2016, Schwarze et al. 2016). The application of such RF-fields has become a widely used tool to distinguish between a magnetic inclination compass based on a radical-pair process and one based on magnetite-based magnetoreception (Henbest et al. 2004). RF-fields are commonly found in virtually all indoor environments that are not specifically shielded with a Faraday cage or where no specific precautions have been taken to exclude such disturbances, for example by avoiding alternate current (AC) power sources. Thus, the presence of RF-fields might be the reason for many failures to demonstrate magnetic orientation in various organisms (Phillips et al. 2013).

We cannot exclude the possibility that electromagnetic disturbances in the radio frequencies were present in the holding or testing rooms in the early orientation studies carried out at Stensoffa. Recent measurements recorded baseline RF-fields below 0.01 nT (see Fig. S3 in Muheim et al. 2016), which is well below the values known to disrupt magnetic compass orientation of birds (peak intensities > 0.1 nT; Ritz et al. 2004, 2009, Muheim et al. 2016, Schwarze et al. 2016). Still, RF-fields produced locally by the equipment (automatic registration cages, light sources, electric heaters, etc.) were possibly present in the majority of the earlier experiments carried out at Stensoffa. When we became aware of the problem in 2003, we made several adjustments in both the bird holding and testing rooms to reduce electromagnetic disturbances, i.e. we removed refrigerator and freezer from the holding room, moved the registration system and the power supply for the magnetic coil to a more distant room, and repositioned all power cords so that no unintentional ground loops arose. Between autumn 2009 and 2011, we carried out a series of experiments with European robins indoors under 521 nm, green lights in a wooden shed in which all incoming AC was filtered and all electric equipment near the testing area, like the light source, was powered by 12 V car batteries. The birds were repeatedly tested with magnetic North aligned towards either one of the four cardinal geographic directions (mN at gN, gE, gS or gW). The magnetic coils used to produce the test fields were grounded and powered by car batteries (cf. Muheim et al. 2016). Despite the effort to reduce any RF-contamination, none of the groups of robins tested in these experiments showed a consistent response relative to the magnetic field (Table 3), indicating that the birds either still had difficulties to use their magnetic compass or that other, still unknown factors lead to the poor orientation.

Conclusions

Despite much effort by different scientists to exclude or control for possible factors that might contribute to the anomalous magnetic orientation at Stensoffa, it has remained difficult to record well-directed magnetic compass orientation in the seasonal appropriate migratory direction at this site. It has to be noted, however, that many orientation experiments performed at Stensoffa have been conducted outdoors, from the early experiments by Alerstam and Högstedt (1983) to more recent experiments (Ilieva et al. 2012, Åkesson et al. 2015). Many of the clear sky experiments have led to significant mean orientation, however often directed towards the setting sun (Sandberg et al. 1988, Åkesson 1993, 1994, Åkesson and Sandberg 1994, Åkesson and Bäckman 1999). Still, the birds show overall more concentrated orientation when they have access to celestial cues in addition to the magnetic information. This, however, does not explain why it is so difficult to demonstrate magnetic compass orientation at Stensoffa. The majority of the proposed explanations for the poor magnetic compass orientation can be essentially excluded, like difficulties to extract magnetic compass information at high latitudes, methodological or experimenter biases, holding duration and repeated testing of individual birds, effects of magnetic anomalies and temporal variations of the ambient magnetic field, and anthropogenic electromagnetic disturbances. The geographic location of southern Sweden might possibly affect the orientation behaviour of birds captured and/or tested at coastal sites, like Falsterbo and Ottenby. However, further investigations are needed to identify the reasons for the poor magnetic compass orientation found in migratory songbirds tested in southern Sweden in general, and at Stensoffa in particular.

Acknowledgements – We would like to thank Thomas Alerstam for establishing orientation research in Lund and for his initial idea to write a paper on the orientation problems at Stensoffa in 2003. We were all fortunate to have him as our doctoral supervisor and be able to learn about bird migration research from one of the most knowledgeable scientist in this field. We would like to thank him for all his support, continuous encouragement and enthusiasm, also when the birds were not oriented towards the seasonal appropriate directions. Not the least, we thank him for numerous fascinating discussions on bird migration and orientation over the past decades. We are very grateful to Felix Liechti, Frank Moore and Åke Lindström for valuable comments on the manuscript. Our work has been supported by various grants from the Swedish Research Foundation (Vetenskapsrådet, VR). Previously unpublished work has been funded by VR 2007-5700, 2011-4765 and 2015-04869 to RM. This report also received support from the Centre for Animal Movement Research (CAnMove) financed by a Linnaeus grant (349-2007-8690) from the Swedish Research Council and Lund Univ. This is report no. 307 from Falsterbo Bird Observatory and report no. 299 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. and Sandberg, R. 1994. Migratory orientation of passerines at dusk, night and dawn. – *Ethology* 98: 177–191.
- Åkesson, S. and Bäckman, J. 1999. Orientation in pied flycatchers: the relative importance of magnetic and visual information at dusk. – *Anim. Behav.* 57: 819–828.
- Åkesson, S., Karlsson, L., Pettersson, J. and Walinder, G. 1992. Body composition and migration strategies: a comparison between robins, *Erithacus rubecula*, from two stop-over sites in Sweden. – *Vogelwarte* 36: 188–195.
- Åkesson, S., Ottosson, U. and Sandberg, R. 1995. Bird orientation: displacement experiments with young autumn migrating wheatears, *Oenanthe oenanthe*, along the Arctic coast of Russia. – *Proc. R. Soc. B* 262: 189–195.
- Åkesson, S., Karlsson, L., Walinder, G. and 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., 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. B* 268: 1907–1913.
- Åkesson, S., Morin, J., Muheim, R. and Ottosson, U. 2005. Dramatic orientation shift of white-crowned sparrows displaced across longitudes in the high arctic. – *Curr. Biol.* 15: 1591–1597.
- Åkesson, S., Odin, C., Hegedüs, R., Ilieva, M., Sjöholm, C., Farkas, A. and Horváth, G. 2015. Testing avian compass calibration: comparative experiments with diurnal and nocturnal passerine migrants in south Sweden. – *Biol. Open* 4: 35–47.
- Alerstam, T. 1978. Reoriented bird migration in coastal areas: dispersal to suitable resting grounds? – *Oikos* 30: 405–408.
- Alerstam, T. 1987. Bird migration across a strong magnetic anomaly? – *J. Exp. Biol.* 130: 63–86.
- Alerstam, T. and Högstedt, G. 1983. The role of the geomagnetic field in the development of birds' compass sense. – *Nature* 306: 463–465.
- Bäckman, J., Pettersson, J. and Sandberg, R. 1997. The influence of fat stores on magnetic orientation in day-migrating chaffinches, *Fringilla coelebs*. – *Ethology* 103: 247–256.
- Batschelet, E. 1981. Circular statistics in biology. – Academic Press.
- Becker, M. 1991. Pigeon orientation: daily variation between morning and noon occur in some years, but not in others. – *Naturwissenschaften* 78: 426–428.
- Bianco, G., Ilieva, M., Veibäck, C., Öfjäll, K., Gadomska, A., Hendebj, G., Felsberg, M., Gustafsson, F. and Åkesson, S. 2016. Emlen funnel experiments revisited: methods update for studying compass orientation in songbirds. – *Ecol. Evol.* doi: 10.1002/ece3.2383
- Del Seppia, C., Luschi, P. and Papi, F. 1996. Influence of emotional factors on the initial orientation of pigeons. – *Anim. Behav.* 52: 33–47.
- Deutschlander, M. E. and 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.
- Ehnbo, S., Karlsson, L., Ylvén, R. and Åkesson, S. 1993. A comparison of autumn migration strategies in robins, *Erithacus rubecula*, at a coastal and an inland site in southern Sweden. – *Ring. Migr.* 14: 84–93.
- Emlen, S. T. and Emlen, J. T. 1966. A technique for recording orientation of captive birds. – *Auk* 83: 361–367.
- Engels, S., Schneider, N.-L., Lefeldt, N., Hein, C. M., Zapka, M., Michalik, A., Elbers, D., Kittel, A., Hore, P. J. and Mouritsen, H. 2014. Anthropogenic electromagnetic noise disrupts magnetic compass orientation in a migratory bird. – *Nature* 509: 353–356.
- Fransson, T. and Hall-Karlsson, S. 2008. Swedish ringing atlas. – Stockholm.
- Freaker, M. J., Muheim, R. and Phillips, J. B. 2006. Magnetic maps in animals: a theory comes of age? – *Q. Rev. Biol.* 81: 327–347.
- Gudmundsson, G. A. and Sandberg, R. 2000. Sanderlings, *Calidris alba*, have a magnetic compass: orientation experiments during spring migration in Iceland. – *J. Exp. Biol.* 203: 3137–3144.
- Helbig, A. J. 1991. Experimental and analytical techniques used in bird orientation research. – In: Berthold, P. (ed.), *Orientation in birds*. Birkhäuser, pp. 271–306.
- Henbest, K. B., Rodgers, C. T., Hore, P. J. and Timmel, C. R. 2004. Radio frequency magnetic field effects on a radical recombination reaction: a diagnostic test for the radical pair mechanism. – *J. Am. Chem. Soc.* 126: 8102–8103.
- Ilieva, M., Toews, D. P. L., Bensch, S., Sjöholm, C. and Åkesson, S. 2012. Autumn migratory orientation and displacement responses of two willow warbler subspecies (*Phylloscopus trochilus trochilus* and *P. t. acredula*) in south Sweden. – *Behav. Process.* 91: 253–261.
- Karlsson, H., Bäckman, J., Nilsson, C. and Alerstam, T. 2010. Exaggerated orientation scatter of nocturnal passerine migrants close to breeding grounds: comparisons between seasons and latitudes. – *Behav. Ecol. Sociobiol.* 64: 2021–2031.
- Karlsson, L., Persson, K., Pettersson, J. and Walinder, G. 1988. Fat-weight relationships and migratory strategies in the robin, *Erithacus rubecula*, at two stop-over sites in south Sweden. – *Ring. Migr.* 9: 160–168.
- Kavokin, K., Chernetsov, N., Pakhomov, A., Bojarinova, J., Kobylkov, D. and Namozov, B. 2014. Magnetic orientation of garden warblers (*Sylvia borin*) under 1.4 MHz radiofrequency magnetic field. – *J. R. Soc. Interface* 11: 20140451.
- Keeton, W. T., Larkin, T. S. and Windsor, D. M. 1974. Normal fluctuations in the earth's magnetic field influence pigeon orientation. – *J. Comp. Physiol. A* 95: 95–103.
- Kiepenheuer, J. 1982. Pigeon orientation: a preliminary evaluation of factors involved or not involved in the detector loft effect. – In: Pap, F. and Wallraff, H. G. (eds), *Avian navigation*. Springer, pp. 203–210.
- Kiepenheuer, J. 1986. A further analysis on the orientation behaviour of homing pigeons behaviour of homing pigeons released within magnetic anomalies. – In: Maret, G., Boccara, N. and Kiepenheuer, J. (eds), *Biophysical effects of steady magnetic fields*. Springer, pp. 148–153.
- Lednor, A. J. and Walcott, C. 1988. Orientation of homing pigeons at magnetic anomalies. – *Behav. Ecol. Sociobiol.* 22: 3–8.
- Lefeldt, N., Dreyer, D., Schneider, N.-L., Steenken, F. and Mouritsen, H. 2015. Migratory blackcaps tested in Emlen funnels can orient at 85 degrees but not at 88 degrees magnetic inclination. – *J. Exp. Biol.* 218: 206–211.
- Moore, F. R. 1977. Geomagnetic disturbance and the orientation of nocturnally migrating birds. – *Science* 196: 682–684.
- Mouritsen, H., Feenders, G., Hegemann, A. and Liedvogel, M. 2009. Thermal paper can replace typewriter correction paper in Emlen funnels. – *J. Ornithol.* 150: 713–715.
- Muheim, R. and Jenni, L. 1999. Nocturnal orientation of robins, *Erithacus rubecula*: birds caught during migratory flight are disoriented. – *Acta Ethol.* 2: 43–50.
- Muheim, R. and Åkesson, S. 2002. Clock-shift experiments with Savannah sparrows, *Passerculus sandwichensis*, at high northern latitudes. – *Behav. Ecol. Sociobiol.* 51: 394–401.
- Muheim, R., Jenni, L. and Weindler, P. 1999. The orientation behaviour of chaffinches, *Fringilla coelebs*, caught during active migratory flight, in relation to the sun. – *Ethology* 105: 97–110.

- Muheim, R., Bäckman, J. and Åkesson, S. 2002. Magnetic compass orientation in European robins is dependent on both wavelength and intensity of light. – *J. Exp. Biol.* 205: 3845–3856.
- Muheim, R., Phillips, J. B. and Åkesson, S. 2006. Polarized light cues underlie compass calibration in migratory songbirds. – *Science* 313: 837–839.
- Muheim, R., Phillips, J. B. and Deutschlander, M. E. 2009. White-throated sparrows calibrate their magnetic compass by polarized light cues during both autumn and spring migration. – *J. Exp. Biol.* 212: 3466–3472.
- Muheim, R., Henshaw, I., Sjöberg, S. and Deutschlander, M. E. 2014. BirdOriTrack: a new video-tracking program for orientation research with migratory birds. – *J. Field Ornithol.* 85: 91–105.
- Muheim, R., Sjöberg, S. and Pinzon-Rodriguez, A. 2016. Polarized light modulates light-dependent magnetic compass orientation in birds. – *Proc. Natl Acad. Sci. USA* 113: 1654–1659.
- Nievergelt, F. and Liechti, F. 2000. Methodische Aspekte zur Untersuchung der Zugaktivität im Emlen-Trichter. – *J. Ornithol.* 141: 180–190.
- Nilsson, C. and Sjöberg, S. 2016. Causes and characteristics of reverse bird migration: an analysis based on radar, radio tracking and ringing at Falsterbo, Sweden. – *J. Avian Biol.* 47: 354–362.
- Payevsky, V. A. 1998. Age structure of passerine migrants at the eastern Baltic coast: the analysis of the coastal effect. – *Ornis Svecica* 8: 171–178.
- Pesnell, W. D. 2015. Solar dynamics observatory (SDO). – In: Pelton, J. N. and Allahdadi, F. (eds), *Handbook of cosmic hazards and planetary defense*. Springer, pp. 179–196.
- Pettersson, J. and Lindholm, C. G. 1983. The sequential passage of different robin, *Erithacus rubecula*, populations at Ottenby. – *Ornis Fenn.* 3: 34–36.
- Pettersson, J. and Hasselquist, D. 1985. Fat deposition and migration capacity of robins, *Erithacus rubecula*, and goldcrests, *Regulus regulus*, at Ottenby, Sweden. – *Ring. Migr.* 6: 66–76.
- Pettersson, J., Hjort, C., Lindström, Å. and Hedenström, A. 1990. Övernitrande rödhakar, *Erithacus rubecula*, kring Medelhavet och flyttande rödhakar vid Ottenby – en morfologisk jämförelse och analys av sträckbilden. – *Vår Fågelvärld* 49: 267–278.
- Phillips, J. B. 1996. Magnetic navigation. – *J. Theor. Biol.* 180: 309–319.
- Phillips, J. B., Schmidt-Koenig, K. and Muheim, R. 2006. True navigation: sensory basis of gradient maps. – In: Brown, M. F. and Cook, R. G. (eds), *Animal spatial cognition: comparative, neuronal and computational approaches*. Comparative Cognition Press. Cyber-book: <www.pigeon.psy.tufts.edu/index.php?content=animal_spatial_cognition>.
- Phillips, J. B., Youmans, P. W., Muheim, R., Sloan, K. A., Landler, L., Painter, M. S. and Anderson, C. R. 2013. Rapid learning of magnetic compass direction by C57BL/6 mice in a 4-armed 'plus' water maze. – *PLoS One* 8: e73112.
- Rakhimberdiev, E., Karagicheva, J., Jaatinen, K., Winkler, D. W., Phillips, J. B. and Piersma, T. 2014. Naïve migrants and the use of magnetic cues: temporal fluctuations in the geomagnetic field differentially affect male and female ruff, *Philomachus pugnax*, during their first migration. – *Ibis* 156: 864–869.
- Ralph, J. C. 1978. Disorientation and possible fate of young passerine coastal migrants. – *Bird-Banding* 49: 237–247.
- Richardson, W. J. 1976. Autumn migration over Puerto Rico and the western Atlantic: a radar study. – *Ibis* 118: 309–332.
- Ritz, T., Thalau, P., Phillips, J. B., Wiltschko, R. and Wiltschko, W. 2004. Resonance effects indicate a radical-pair mechanism for avian magnetic compass. – *Nature* 429: 177–180.
- Ritz, T., Wiltschko, R., Hore, P. J., Rodgers, C. T., Stapput, K., Timmel, C. R. and Wiltschko, W. 2009. Magnetic compass of birds is based on a molecule with optimal directional sensitivity. – *Biophys. J.* 96: 3451–3457.
- Sandberg, R. and Moore, F. R. 1996. Migratory orientation of red-eyed vireo, *Vireo olivaceus*, in relation to energetic condition and ecological context. – *Behav. Ecol. Sociobiol.* 39: 1–10.
- Sandberg, R. and Pettersson, J. 1996. Magnetic orientation of snow buntings (*Plectrophenax nivalis*), a species breeding in the high Arctic: passage migration through temperate-zone areas. – *J. Exp. Biol.* 199: 1899–1905.
- Sandberg, R., Pettersson, J. and Alerstam, T. 1988. Why do migrating robins, *Erithacus rubecula*, captured at two nearby stop-over sites orient differently? – *Anim. Behav.* 36: 865–876.
- Sandberg, R., Ottosson, U. and Pettersson, J. 1991. Magnetic orientation of migratory wheatears, *Oenanthe oenanthe*, in Sweden and Greenland. – *J. Exp. Biol.* 155: 51–64.
- Sandberg, R., Bäckman, J. and Ottosson, U. 1998. Orientation of snow buntings, *Plectrophenax nivalis*, close to the magnetic north pole. – *J. Exp. Biol.* 201: 1859–1870.
- Sandberg, R., Bäckman, J., Moore, F. R. and Lohmus, M. 2000. Magnetic information calibrates celestial cues during migration. – *Anim. Behav.* 60: 453–462.
- Sandberg, R., Moore, F. R., Bäckman, J. and Lohmus, M. 2002. Orientation of nocturnally migrating Swainson's thrush at dawn and dusk: importance of energetic condition and geomagnetic cues. – *Auk* 119: 201–209.
- Schiffner, I. and Wiltschko, R. 2011. Temporal fluctuations of the geomagnetic field affect pigeons' entire homing flight. – *J. Comp. Physiol. A* 197: 765–772.
- Schwarze, S., Schneider, N.-L., Reichl, T., Dreyer, D., Lefeldt, N., Engels, S., Baker, N., Hore, P. J. and Mouritsen, H. 2016. Weak broadband electromagnetic fields are more disruptive to magnetic compass orientation in a night-migratory songbird (*Erithacus rubecula*) than strong narrow-band fields. – *Front. Behav. Neurosci.* 10: 55.
- Sjöberg, S., Alerstam, T., Åkesson, S., Schulz, A., Weidauer, A., Coppack, T. and Muheim, R. 2015. Weather and fuel reserves determine departure and flight decisions in passerines migrating across the Baltic Sea. – *Anim. Behav.* 104: 59–68.
- Tenforde, T. S. 1995. Spectrum and intensity of environmental electromagnetic fields from natural and man-made sources. – In: Blank, M. (ed.), *Electromagnetic fields: biological interactions and mechanisms*. American Chemical Society, pp. 13–35.
- Wagner, G. 1983. Natural geomagnetic anomalies and homing in pigeons. – *Comp. Biochem. Physiol.* 76A: 691–701.
- Weindler, P., Beck, W., Liepa, V. and Wiltschko, W. 1995. Development of migratory orientation in pied flycatcher in different magnetic inclinations. – *Anim. Behav.* 49: 227–234.
- Wiltschko, W. 1968. Über den Einfluss statischer Magnetfelder auf die Zugorientierung der Rotkehlchen, *Erithacus rubecula*. – *Z. Tierpsychol.* 25: 537–558.
- Wiltschko, W. 1978. Further analysis of the magnetic compass of migratory birds. – In: Schmidt-Koenig, K. and Keeton, W. T. (eds), *Animal migration, navigation and homing*. Springer, pp. 301–310.
- Wiltschko, W. and Wiltschko, R. 1972. Magnetic compass of European robins. – *Science* 176: 62–64.
- Wiltschko, W. and Wiltschko, R. 1995. Migratory orientation of European robins is affected by the wavelength of light as well as by a magnetic pulse. – *J. Comp. Physiol. A* 177: 363–369.
- Wiltschko, W., Nohr, D., Füller, E. and Wiltschko, R. 1986. Pigeon homing: the use of magnetic information in position finding. – In: Maret, G., Boccarda, N. and Kiepenheuer, J. (eds), *Biophysical effects of steady magnetic fields*. Springer, pp. 154–162.

- Wiltschko, W., Munro, U., Beason, R. C., Ford, H. and Wiltschko, R. 1994. A magnetic pulse leads to a temporary deflection in the orientation of migratory birds. – *Experientia* 50: 679–700.
- Wiltschko, W., Wiltschko, R. and Munro, U. 2000. Light-dependent magnetoreception in birds: the effect of intensity of 565-nm green light. – *Naturwissenschaften* 87: 366–369.
- Wiltschko, W., Gesson, M. and Wiltschko, R. 2001. Magnetic compass orientation of European robins under 565 nm green light. – *Naturwissenschaften* 88: 387–390.
- Wiltschko, W., Stapput, K., Thalau, P. and Wiltschko, R. 2006. Avian magnetic compass: fast adjustment to intensities outside the normal functional window. – *Naturwissenschaften* 93: 300–304.