Calibration of magnetic and celestial compass cues in migratory birds - a review of cue-conflict experiments

Muheim, Rachel; Moore, F R; Phillips, J B

Published in:
Journal of Experimental Biology

DOI:
10.1242/jeb.01960

2006

Citation for published version (APA):
Muheim, R., Moore, F. R., & Phillips, J. B. (2006). Calibration of magnetic and celestial compass cues in migratory birds - a review of cue-conflict experiments. *Journal of Experimental Biology*, *209*(1), 2-17. https://doi.org/10.1242/jeb.01960

Total number of authors:
3

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

The Journal of Experimental Biology 209, 2-17
Published by The Company of Biologists 2006
doi:10.1242/jeb.01960

Review

Calibration of magnetic and celestial compass cues in migratory birds – a review of cue-conflict experiments

Rachel Muheim[1,2,*], Frank R. Moore[3] and John B. Phillips[2]

[1]Department of Animal Ecology, Lund University, SE-223 62 Lund, Sweden, [2]Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061-0406, USA and [3]Department of Biological Sciences, University of Mississippi, Hattiesburg, MS 39406-5018, USA

*Author for correspondence at address 2 (e-mail: rmuheim@vt.edu)

Accepted 25 October 2005

Summary

Migratory birds use multiple sources of compass information for orientation, including the geomagnetic field, the sun, skylight polarization patterns and star patterns. In this paper we review the results of cue-conflict experiments designed to determine the relative importance of the different compass mechanisms, and how directional information from these compass mechanisms is integrated. We focus on cue-conflict experiments in which the magnetic field was shifted in alignment relative to natural celestial cues. Consistent with the conclusions of earlier authors, our analyses suggest that during the premigratory season, celestial information is given the greatest salience and used to recalibrate the magnetic compass by both juvenile and adult birds. Sunset polarized light patterns from the region of the sky near the horizon appear to provide the calibration reference for the magnetic compass. In contrast, during migration, a majority of experiments suggest that birds rely on the magnetic field as the primary source of compass information and use it to calibrate celestial compass cues, i.e. the relative saliency of magnetic and celestial cues is reversed. An alternative possibility, however, is suggested by several experiments in which birds exposed to a cue conflict during migration appear to have recalibrated the magnetic compass, i.e. their response is similar to that of birds exposed to cue conflicts during the premigratory season.

The general pattern to emerge from these analyses is that birds exposed to the cue conflict with a view of the entire sunset sky tended to recalibrate the magnetic compass, regardless of whether the cue conflict occurred during the premigratory or migratory period. In contrast, birds exposed to the cue conflict in orientation funnels and registration cages that restricted their view of the region of sky near the horizon (as was generally the case in experiments carried out during the migratory season) did not recalibrate the magnetic compass but, instead, used the magnetic compass to calibrate the other celestial compass systems. If access to critical celestial cues, rather than the timing of exposure to the cue conflict (i.e. premigratory *vs* migratory), determines whether recalibration of the magnetic compass occurs, this suggests that under natural conditions there may be a single calibration reference for all of the compass systems of migratory birds that is derived from sunset (and possibly also sunrise) polarized light cues from the region of sky near the horizon.

In cue-conflict experiments carried out during the migratory season, there was also an interesting asymmetry in the birds' response to magnetic fields shifted clockwise and counterclockwise relative to celestial cues. We discuss two possible explanations for these differences: (1) lateral asymmetry in the role of the right and left eye in mediating light-dependent magnetic compass orientation and (2) interference from the spectral and intensity distribution of skylight at sunset with the response of the light-dependent magnetic compass.

Key words: migratory orientation, compass calibration, cue conflict, magnetic compass, celestial compass.

Introduction

Migrating birds have an inherited migratory program coding the general direction and distance to be travelled (reviewed by Berthold, 1991, 1996; Gwinner, 1996), and they use several different compass systems to determine the seasonally appropriate migratory direction. They use compass information derived from the geomagnetic field (reviewed by Wiltschko and Wiltschko, 1995), star patterns (Sauer, 1957;

Emlen, 1975), the sun's position at sunset (Moore, 1987; see also Schmidt-Koenig, 1990) and patterns of skylight polarization (Able, 1982; Moore and Phillips, 1988; Helbig, 1991; Phillips and Moore, 1992). In order to maintain an accurate heading when changing weather conditions alter celestial cue availability and/or when directional information between compass systems diverges (e.g. because magnetic declination, the difference between magnetic and geographic north, varies globally), the compass systems used by birds must be 'calibrated' with respect to a common reference system. This reference system may be one of the compass systems that has primacy over the others, or it may be an independent source of directional information. The simplest case would be a single reference system that is either (1) available prior to migration (if the initial calibration of the compass systems is retained throughout the migration) or (2) accessible on a regional or global scale (if the calibration of the compass systems is updated periodically during migration). Previous reviews of the compass calibration literature (Able, 1993; Åkesson, 1994; Wiltschko et al., 1997, 1998a; Wiltschko and Wiltschko, 1999) suggest that such schemes based on a single reference system may be overly simplistic, given the complex demands that long-distance migration places on the birds' orientation systems. Nevertheless, our reanalysis of the literature on cue calibration adds credence to the possibility of a single underlying reference system for calibration of the compass systems of migratory birds.

Cue-conflict experiments

For decades, orientation researchers have been interested in the interrelationships among the different compass systems used by migratory birds. These interrelationships have typically been investigated in experiments in which birds were given conflicting directional information from two or more cues to determine which of the conflicting cues is given greater saliency by the migrants under different conditions, and whether the conflict results in a persistent change ('recalibration') of the directional information derived from one or more of the compass systems. Cue conflicts were created by (1) artificially shifting the horizontal component of the magnetic field relative to celestial cues, (2) shifting celestial cues (e.g. altering sun position with mirrors, creating an artificial skylight polarization pattern with polarizing filters that could be rotated to different alignments, or rotating an artificial starry sky) while exposing the birds to the natural geomagnetic field, or combinations of both treatments.

The findings of cue-conflict experiments have varied considerably, in some cases appearing to yield conflicting results (for reviews, see Åkesson, 1994; Wiltschko et al., 1997, 1998a; Wiltschko and Wiltschko, 1999). In the present review we focus on the relationships between the magnetic compass and natural celestial cues (sun, polarized light patterns and stars). In the main analyses, we have only included experiments in which the direction of the horizontal component of the magnetic field vector was shifted relative to natural celestial cues. Thus, experiments manipulating the polarization pattern with artificial polarizing or depolarizing filters were not included in these analyses because polarization filters alter the natural polarization pattern considerably (e.g. changing the intensity and spectral properties of polarization, as well as artificially increasing the axial symmetry of the overall pattern), with unknown effects on the orientation systems of birds. Mirror experiments were also excluded because rotation of celestial cues was necessarily limited to the regions of the sky near the horizon, and because mirrors used in such experiments were made of non-ultraviolet transmitting glass (normal window glass) with the reflecting layer on the back surface, and thus are likely to have reduced the relative intensity of ultraviolet light, which has been suggested to play a role in polarized light detection by birds (Phillips and Waldvogel, 1988). Also experiments performed under artificial star patterns were excluded, because of differences from the natural sky. Our aim was to find general patterns that could help to explain the wide variety of different (sometimes apparently conflicting) results in the literature concerning the use of magnetic and celestial cues.

We divided the studies/experiments into three groups:

(1) After-effects of premigratory exposure to cue conflict (12 experiments). Juvenile birds raised in captivity or adult birds caught during the breeding period were exposed to a cue-conflict situation during the premigratory period. Later, once the birds had initiated seasonal migratory activity, the after-effects of the cue conflict were tested in orientation funnels to determine whether the use of a particular cue was affected, either alone or in combination with other cue(s).

(2) Effects of exposure to cue conflict during migration (46 experiments). Birds (either inexperienced juveniles or experienced adults) caught during migration were exposed to a cue conflict while being tested in orientation funnels, to determine whether the birds preferentially use a particular cue or combination of cues.

(3) After-effects of exposure to cue conflict during migration (18 experiments). Birds that were exposed to a cue conflict during the migratory season were subsequently tested in the absence of the cue conflict, either by being released after dark with light capsules that permitted visual observation of vanishing bearings and/or with transmitters that permitted radio tracking of the subsequent migratory paths, or by being tested in orientation funnels in some cases with a restricted subset of cues available.

The premigratory period was defined as the time during which the birds did not show migratory restlessness, and the migratory period as the period during which the birds increased their fat reserves and exhibited migratory restlessness. We discuss the following variables in our analyses: species, age, experimental season, testing location (place), direction of shift [clockwise (CW) or counterclockwise (CCW)], magnitude of shift, available cues during the cue conflict, type of experiment (i.e. cues available during testing of migratory response).

Cue calibration during premigratory and migratory period

After-effects of premigratory exposure to cue conflict

After exposure to the cue conflict during the premigratory periods, the birds in a majority of experiments were shown to have recalibrated their magnetic compass when subsequently tested during the migratory season (Bingman, 1983; Prinz and Wiltschko, 1992; Able and Able, 1993; Weindler and Liepa, 1999; Table 1)[†]. That is, when subsequently tested with only magnetic cues available, birds having had access to celestial cues that included sunrise and sunset during the premigratory exposure were shown to have recalibrated their magnetic compass in 5 out of 6 cases (Table 1Ac,d, Table 1Ba,c–e). In all but one of the cases that showed recalibration of the magnetic compass, the birds were exposed to the cue conflict in cages that provided a full view of the sky (see below). An effect of the cue conflict was not evident when the birds were tested in a vertical magnetic field with access to the natural sky, indicating that the calibration of the birds' celestial compasses had not been affected (Bingman, 1984; Able and Able, 1997; Table 1Aa,b). In the one test in which birds were exposed to the cue conflict at times of day that did not include sunrise and sunset, subsequent tests carried out during the migratory season showed no evidence of recalibration of the magnetic compass (Table 1Bb).

The one inconsistency in this pattern can be found in the study by Able and Able (1990b; Table 1Ba–c) that exposed three groups of Savannah sparrows *Passerculus sandwichensis* with access to different celestial cues, to a shifted magnetic field. One group was exposed for continuous periods around the clock to all available celestial cues, i.e. sunrise, sun, sunset and stars (Table 1Ba). A second group was placed into the outdoor cage at night only, i.e. was allowed to experience the starry sky only, but no daytime and twilight cues (Table 1Bb). The third group was exposed to the cue conflict during daytime only, from prior to sunrise to after sunset (Table 1Bc). According to Able and Able (1990b), all groups recalibrated their magnetic compass when later tested during the migration season indoors with access to magnetic field cues only. However, they chose a control group that had never experienced a natural sky, while all the experimental groups had experienced natural celestial cues. We, therefore, considered Able and Able's 'natural day sky group', which had experienced the natural day sky in an unshifted magnetic field, as a more appropriate control group. With this group as the control, only the experimental group experiencing all celestial cues (Table 1Ba) recalibrated the magnetic compass, while the other two groups (Table 1Bb,c) did not significantly shift direction, despite the fact that the third group (Table 1Bc) had access to both sunrise and sunset cues.

Interestingly, Prinz and Wiltschko (1992) observed recalibration of the magnetic compass only when the magnetic field was shifted CCW relative to the celestial cues (Table 1Ad). The birds were disoriented when the field shift was CW (Table 1Cc). This indicates a possible asymmetry in the birds' response depending on the direction of shift (see also evidence of an asymmetry in response to cue conflicts during migration).

At a first glance, the study by Alerstam and Högstedt (1983) also appears to be an exception to the general pattern discussed above, although the absence of significant orientation by controls prevents firm conclusions (Table 1Ca,b). They exposed pied flycatchers *Ficedula hypoleuca* during their nestling period to CW and CCW shifted magnetic fields in the nest boxes. The birds were then held in an enclosed room without access to celestial cues until the onset of autumn migratory restlessness. When the birds were tested outdoors under natural celestial and magnetic cues, they exhibited shifts in orientation that appeared to be consistent with celestial compass cues being recalibrated with respect to the rotated magnetic fields. Thus, they did not appear to recalibrate their magnetic compass as observed in the other experiments in which birds were exposed to a shifted magnetic field during the premigratory season. However, a closer look at the methods suggests a simple explanation for this apparent contradiction. The magnetic coils used to shift the magnetic field around the nest boxes were paired Helmholz coils attached to the lower part of the nest boxes (see picture published in Alerstam and Högstedt, 1983). Due to the size and location of the coils, the nest box entrances were not exposed to the magnetic field inside the coils, but to the field outside of the radius of the coils looping back in the opposite direction. Nestlings sitting at the nest entrance were therefore exposed to a shift in the magnetic field that was smaller in magnitude (i.e. 45–50°) and in the opposite direction from the intended one. Consequently, the shifts in direction observed in these experiments were consistent with the nestlings recalibrating the magnetic compass at the nest box entrance where they had access to celestial cues.

Effects of exposure to cue conflict during migration

In these experiments birds were tested during the migratory season while being exposed to a shifted magnetic field and natural celestial cues. In the majority of experiments that yielded meaningful results (see below), the birds shifted their orientation in accordance with the rotated magnetic field (Table 2A) indicating that they were using the magnetic field as the primary orientation cue.

A subset of experiments could not be included in the above analysis. In the experiments shown in Table 2B the orientation of both the control and experimental group was not significantly different from the position of sunset and was not directed into the species-specific migratory direction. It appears likely that phototactic behaviour towards the setting

---

[†] Unfortunately, the number of studies examining premigratory exposure to cue conflicts is limited and the birds in several studies exhibited bimodal orientation in the control and/or experimental group (Tables 1, 2), so that it was not possible to determine whether experimentals were shifted CW or CCW relative to controls (Bingman, 1983; Able and Able, 1990b, 1993). Still, as long as subsequent experiments were performed indoors with only the magnetic field available as orientation cue, a significant shift in direction between control and experimental group indicates a recalibration of the magnetic compass.

Table 1. *After-effects of premigratory exposure to cue conflicts, including studies where birds were exposed to deflected magnetic fields before the onset of the autumn migratory period*

	Reference	Species (age)	Place	Magnetic field shift	Response	Significance of control/ experiment	Celestial cue(s) available during calibration	View of sky	Type of experiment	Magnetic compass recalibrated	Celestial compass recalibrated
(A) Both experimental and control groups significantly unimodally oriented, with controls oriented in the seasonally appropriate migratory direction											
a	Bingman, 1984	Pied flycatcher (juv)	DEU	105° CCW	49° CW^{ns}	Y/Y	All	Full	Vertical magnetic field		N
b	Able and Able, 1997	Savannah sparrow (juv)	USA	90° CW	20° CW^{ns}	Y/Y	Sunrise/sun/sunset	Full	Vertical magnetic field		N
c	Weindler and Liepa, 1999	Pied flycatcher (ad)	LVA	90° CCW	67° CW**	Y/Y	All	Full	Indoors	Y	
d	Prinz and Wiltschko, 1992	Pied flycatcher (juv)	DEU	120° CCW	119° CW***	Y/Y	All	Full	Simulated overcast	Y	
(B) Direction of shift in orientation not discernible because of bimodal response(s)											
a	Able and Able, 1990b	Savannah sparrow (juv)	USA	110° CW	34° CW/146° CCW*	Y[1]/Y	All	Full	Indoors	Y	
b	Able and Able, 1990b	Savannah sparrow (juv)	USA	110° CW	10° CW/170° CCW^{ns}	Y[1]/Y	Stars	Full	Indoors	N	
c	Able and Able, 1990b	Savannah sparrow (juv)	USA	110° CW	10° CW/170° CCW^{ns}	Y[1]/Y	Sunrise/sun/sunset	Full	Indoors	N	
d	Bingman, 1983	Savannah sparrow (juv)	USA	90° CCW	90° CW/CCW***	Y/Y	All	Full	Indoors	Y	
e	Able and Able, 1993	Savannah sparrow (juv)	USA	90° CCW	73° CCW/107° CW ***	Y/Y	Sunrise/sun/sunset	Funnel	Indoors	Y	
(C) Control/experimental groups not significantly oriented											
a	Alerstam and Högsted, 1983	Pied flycatcher (juv)	SWE	90° CW[2]	(77° CW)*	N/Y	All	Nesthole	Natural conditions		
b	Alerstam and Högsted, 1983	Pied flycatcher (juv)	SWE	90° CCW[2]	(124° CCW)***	N/Y	All	Nesthole	Natural conditions		
c	Prinz and Wiltschko, 1992	Pied flycatcher (juv)	DEU	120° CW	(135° CW)	Y/N	All	Full	Simulated overcast		

[1] Control group = ‘Natural day sky group’ in Able and Able (1990b), which we consider as a better control than Able’s control group raised entirely indoors.

[2] Direction of shift reverse for birds sitting at hole of nest box (see text).

The age of the tested birds is given when known.

Countries are abbreviated according to the official ISO ALPHA-3 code of the United Nations.

The magnetic field shift is the amount and direction that the artificial magnetic field was shifted relative to celestial cues. For the northern hemisphere, CW shifts correspond to shifts ‘with the sun’ (WS); for the southern hemisphere, they correspond to shifts ‘against the sun’ (AS).

The response specifies the shift of the experimental group relative to the control direction, and statistical significance between the control and experimental groups as reported by the original publication is indicated as follows: $***P<0.001$, $**P<0.01$, $*P\leqslant 0.05$, $^{ns}P>0.05$. Statistical significance (Y; $P\leqslant 0.05$) or insignificance (N; $P>0.05$) of the control and experimental group are also given.

Celestial cues available during conflict include all natural cues provided by the sky during exposure and accessible to the birds (all=sunrise, sun, sunset and stars).

View of sky refers to degrees of visible sky around the zenith during the cue-conflict exposure; full, view from cage not restricting cues close to horizon; funnel, view from funnel (degree of sky not given in original publication).

The type of experiment gives information on the cues available for orientation (simulated overcast and indoor experiments, magnetic cues only; experiments under natural conditions and release experiments, magnetic and celestial cues; experiments in a vertical magnetic field, celestial cues only).

The last two colons indicate whether the magnetic or celestial compass had been recalibrated.

For scientific names of the bird species refer to the original publications.

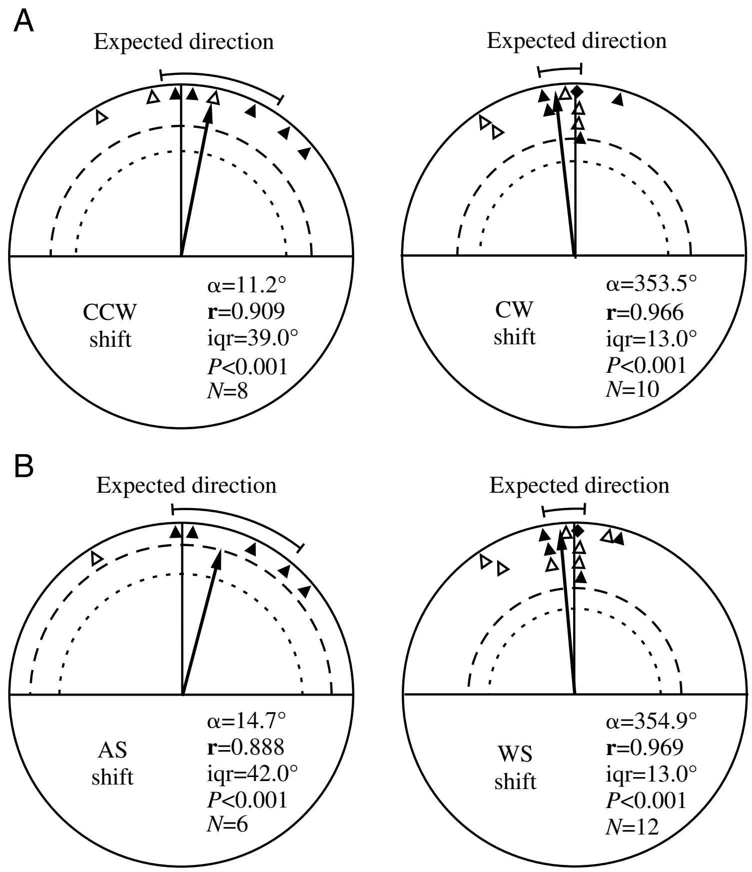

Fig. 1. Deviations from the expected directional shifts of birds that are relying on the magnetic compass in cue conflicts between magnetic and sunset cues during the migratory period (Table 2A, studies not listed in parentheses). The magnetic field shifts are divided into counterclockwise (CCW) and clockwise (CW) shifts and into ‘against the sun’ (AS) and ‘with the sun’ (WS) shifts, since CW and CCW shifts should be interpreted differently by birds living in the northern and southern hemispheres (see text). Filled triangles indicate 90°, open triangles 120° and the rhomboid 115° shifts of the magnetic field. The two half-circles indicate the 0.1% (broken line) and 5% (dotted line) significance level according to the Rayleigh test (Batschelet, 1981). The arrows give the mean direction (α) and their length is proportional to the mean vector length **r** with the radius of the circle=1. Outside of the circle the 50% inter-quartile range (IQR) is indicated. Only included are those studies that exposed the birds to sunset cues and where both control and experimental groups exhibited significant unimodal orientation, with a significant shift between treatments, and the control direction did not coincide with the position of the setting sun (Table 2A, studies not listed in parentheses).

sun predominated over migratory orientation. As a consequence, these responses provide little, if any, information about the compass cues used for migratory orientation. We therefore excluded those experiments from further examination. We also excluded experiments in which either the control and/or experimental group was disoriented (Table 2C). In the case of disorientation, we could not distinguish an effect on the directional information provided by one or more of the compass systems from an effect on the birds’ motivation. We included experiments in the analysis in which the experimental birds oriented towards the setting sun, but not the controls (Table 2Aa,b,d,e,o,p,r), since here the expected direction after the shift could coincide with the sunset position simply by chance, and the response of controls suggested that the birds were exhibiting migratory, rather than phototactic, orientation. We also included two experiments where the control birds oriented into the seasonally appropriate migratory direction, but where this direction happened to coincide with the position of sunset (Table 2Ac,q).

Interestingly, among experiments performed at sunset and resulting in significant shifts (Table 2A, references not in parentheses; see explanation in legend to Table 2), there was an asymmetry in the response of the birds exposed to CW and CCW shifts in the magnetic field. The variability in the responses exhibited by the birds exposed to the CCW rotated magnetic fields was significantly greater than that of birds exposed to the CW rotated fields (comparison of 50% inter-quartile ranges: CW, IQR=13.0°, *N*=10; CCW, IQR=39.0°, *N*=8; *P*=0.05; for statistical reference, see Muheim et al., 1999; Fig. 1A). Wiltschko and co-authors found that the response of Australian silvereyes *Zosterops l. lateralis* to CW and CCW shifted magnetic fields differed from that observed in species tested in the northern hemisphere, and suggested that the reason for this difference might lie in the reverse rotation of the sun in the southern compared to the northern hemisphere (Wiltschko et al., 1998b). To explore this possibility further, we grouped the data in ‘with the sun rotation’ (WS) and ‘against the sun rotation’ (AS). When we tested for variability in the expected shift, we also found a statistically significant difference between the two groups. The AS group was significantly more variable than the WS group (comparison of 50% inter-quartile ranges: WS, IQR=13.0°, *N*=12; AS, IQR=42.0°, *N*=6; *P*=0.04; Fig. 1B).

In addition, among the experiments not included in the above analysis, AS shifts were involved in 9 of the 11 experiments that reported sun attraction in the control and experimental group (Table 2B) and in 3 of the 4 experiments that showed directed orientation in the control group (indicating that the birds were motivated to exhibit migratory orientation), but disorientation in the experimental group (Table 2Cf–i). In Sandberg et al. (2000), the two species exposed to a CCW (AS) shift showed a delayed response to the treatment (Tables 2Bj,k, 3Af,g), while the two species exposed to a CW (WS) shift reacted immediately

(Tables 2Ad,e, 3Ac,d)[‡]. Overall, therefore, the birds reacted to AS shifts less readily, with lower accuracy and less consistency than to WS shifts.

After effects of exposure to cue conflict during migration

In a number of recent experiments, birds were exposed to a cue conflict while being tested in orientation experiments or held in an outdoor cage and later tested in the absence of the cue conflict, either (1) under natural conditions (natural magnetic and celestial cues) in orientation funnels or release experiments, (2) in orientation funnels with access to celestial cues only (vertical magnetic field), or (3) in orientation funnels indoors with only magnetic cues available (Table 3). With four exceptions (see below), all birds continued to exhibit a shift consistent with the rotated magnetic field that they had experienced during the cue conflict. Birds tested in orientation funnels or in release experiments with access to natural magnetic and celestial cues (i.e. with the magnetic field returned to its original alignment) continued to exhibit shifted orientation (Sandberg et al., 2000; Åkesson et al., 2002; Table 3Ac,d,f–h), suggesting that information from the rotated magnetic field experienced during the cue conflict had been transferred to celestial cues (i.e. one or more of the celestial compass systems had been recalibrated). Consistent with recalibration of the celestial compass(es), birds tested in a vertical magnetic field with access only to celestial compass information, also exhibited shifted orientation (Wiltschko et al., 1998b, 1999, 2001; Table 3Ae,i,j,l;). Finally, birds tested after exposure to the cue conflict with only magnetic cues available exhibited orientation that was indistinguishable from controls (Wiltschko et al., 1999; Table 3Ak), confirming that the magnetic compass provided the primary reference system used to establish the migratory direction and was not recalibrated.

There were four exceptions to the general pattern of findings from studies of the after-effects of cue-conflict exposures during the migratory period (i.e. four studies that did not show recalibration of celestial cues relative to magnetic cues). Two exceptions are from a study of Savannah sparrows by Able and Able (1995a; Table 3Ba,b), in which birds were exposed to the cue conflict in outdoor cages with a full view of the sky. Following round-the-clock exposure to 90° CW and CCW shifts of the magnetic field for 4 clear days and nights, a group of juvenile and a group of adult birds tested indoors with only access to magnetic cues exhibited shifts of approximately 90° in both conditions. Although the responses were bimodal, so the direction of shift could not be determined, the correspondence between the magnitude of the shift and the rotation of the magnetic field during the earlier cue conflict suggests that the magnetic compass was recalibrated. In the other two exceptions, Cochran and colleagues (2004) exposed grey-cheeked thrush *Catharus minimus* and Swainson's thrush *Catharus ustulatus* during migration to 70° to 90° CW rotated magnetic fields (Table 3Aa,b). The birds in Cochran et al.'s study were exposed to the cue conflict in outdoor cages in which they had a full view of the entire sky down to the horizon for variable periods up to about 3 h, including sunset. When subsequently released after the sunset period, radio-tracked birds followed tracks consistent with a recalibrated magnetic compass. On subsequent nights after the Swainson's thrushes had experienced the natural (unrotated) magnetic field through one sunrise and sunset period, the shifted orientation of radio-tracked birds was eliminated. Sandberg et al. (2000) carried out a study very similar to Cochran et al. (2004), but instead of using radio telemetry they followed the vanishing directions after releasing the birds (one of the four species used was Swainson's thrush, as in Cochran et al., 2004) with light capsules. Sandberg et al.'s results were comparable to the funnel experiments they carried out with the same individuals during exposure to the cue conflict prior to the release experiments (Table 3Aa,c,d,f,g), i.e. the birds did not recalibrate their magnetic compass. Cochran and colleagues reported that the directions of their thrushes were already deflected from the very beginning of the tracking, which would coincide with the visual observations of the initial orientation of birds carrying light capsules performed by Sandberg et al. (2000). The major difference between the two studies is unlikely to be due to the difference in the methods used to record the data (funnel experiments *vs* radio tracking/release experiment), as suggested by Cochran et al. (2004), but rather to the difference in exposure to the cue conflict (open cage with full view of sky at horizon *vs* view from funnel). Summarising, among the studies of after-effects of cue conflicts carried out during the migratory period, the experiments by Able and Able (1995a) and Cochran et al. (2004) were exceptional in two respects: (1) they were the only studies in which the birds experienced the cue conflict with a full view of the sky down to the horizon, and (2) they were the only studies to show recalibration of the magnetic compass.

Cue calibration in relation to access to celestial cues

The studies by Able and Able (1995a) and Cochran et al. (2004) suggest that recalibration of the magnetic compass may depend not on season (premigratory *vs* migratory), but on access to celestial cues (Table 4).

Cue-conflict exposures are typically carried out in two different ways: (1) by exposing the birds to the shifted magnetic field in outdoor cages with a full view of the surrounding, including the horizon or (2) by exposing them in orientation funnels (Emlen and Emlen, 1966) or octagonal registration cages (Wiltschko et al., 1971; Wiltschko and Höck, 1972; Wiltschko and Wiltschko, 1975a,b) that restrict the view of the celestial cues near the horizon to different degrees. Most funnels allow the birds to view a 120–160° section of the sky centered around the zenith. A few studies have been carried out in funnels with a surrounding shield that allowed the birds

---

[‡] Of the experiments in which controls exhibited significant unimodal orientation, and exposure to the cue conflict included sunset, 9 of 15 groups of birds exposed to a AS-shifted magnetic field compared to only 2 of 14 groups exposed to the WS-shifted magnetic field showed sun attraction (Fisher's exact probability test, $P=0.017$; Table 2B).

Table 2. *Exposure to cue conflicts during migration*

Reference	Species (age)	Season	Place	Shift	Response	Significance of control/ experiment	Celestial cue(s) available during calibration	View of sky around zenith
(A) Both experimental and control groups significantly unimodally oriented, with controls oriented in the seasonally appropriate migratory direction								
(a) Sandberg et al., 1988a,b	European robin (juv+ad)	Spring	SWE	90° CW	32° CCW/148° CW^{ns}	Y/Y^{2}	Sunset/stars	90°
(b) Sandberg et al., 1988a,b	European robin (juv+ad)	Autumn	SWE	90° CW	48° CW/132° CCW^{ns}	Y/Y^{2}	Sunset/stars	90°
c Sandberg and Pettersson, 1996	Snow bunting	Autumn	SWE	90° CW	93° CW**	Y^{1}/Y	Sunset/stars	160°
d Sandberg et al., 2000	Red-eyed vireo	Autumn	USA	90° CW	80° CW**	Y/Y^{2}	Sunset/stars	160°
e Sandberg et al., 2000	Northern waterthrush	Autumn	USA	90° CW	79° CW**	Y/Y^{2}	Sunset/stars	160°
f Sandberg et al., 2002	Swainson's thrush	Autumn	USA	90° CW	106° CW^{3,***}	Y/Y	Sunset/stars	160°
(g) Sandberg et al., 2002	Swainson's thrush	Autumn	USA	90° CW	158° CW^{3,4,***}	Y/Y	Sunrise	160°
h Wiltschko et al., 1971	European robin	Spring	DEU	115° CW	116° CW***	Y/Y	Sunset/stars/sunrise	⩽102°
i Wiltschko and Wiltschko, 1975a	Common whitethroat	Autumn	ESP	120° CW	117° CW***	Y/Y	Sunset/stars/sunrise	95°
j Wiltschko and Wiltschko, 1975a	garden warbler	Autumn	ESP	120° CW	122° CW***	Y/Y	Sunset/stars/sunrise	95°
k Wiltschko and Wiltschko, 1975b	European robin	Spring	ESP	120° CW	86° CW*** d	Y/Y	Sunset/stars/sunrise	95°
(l) Bingman, 1987	European robin	Spring	ITA	120° CW	106° CW** d	Y/Y	Stars	160°
m Bingman and Wiltschko, 1988	Dunnock	Spring	ITA	120° CW	122° CW***	Y^{5}/Y	Sunset/stars	Funnel
n Wiltschko et al., 1998b	Australian silvereye	Spring	AUS	120° CW	88° CW^{6,***} d	Y/Y	Sunset/stars	Funnel
(o) Sandberg et al., 1988a,b	European robin (juv+ad)	Spring	SWE	90° CCW	51° CCW^{ns}	Y/Y^{2}	Sunset/stars	90°
(p) Sandberg et al., 1988a,b	European robin (juv+ad)	Autumn	SWE	90° CCW	23° CW/157° CCW^{ns}	Y/Y^{2}	Sunset/stars	90°
q Åkesson, 1994	Pied flycatcher (juv)	Autumn	SWE	90° CCW	40° CCW*	Y^{1}/Y	Sunset/stars	160°
r Sandberg and Moore, 1996	Red-eyed vireo (juv+ad)	Spring	USA	90° CCW	64° CCW*	Y/Y^{2}	Sunset/stars	160°
s Sandberg and Moore, 1996	Red-eyed vireo (juv+ad)	Autumn	USA	90° CCW	50° CCW^{3,*}	Y/Y	Sunset/stars	160°
t Sandberg and Pettersson, 1996	Snow bunting	Spring	SWE	90° CCW	92° CCW**	Y/Y	Sunset/stars	160°
(u) Gudmundsson and Sandberg, 2000	Sanderling	Spring	ISL	90° CCW	82° CCW^{7,**}	Y/Y	Midnight sun	>130°
v Åkesson et al., 2002	White-crowned sparrow (juv)	Autumn	CAN	90° CCW	86° CCW^{8,***}	Y/Y	Sunset/stars	140°
w Wiltschko et al., 1998b	Australian silvereye	Spring	AUS	120° CCW	150° CCW^{6,***}	Y/Y	Sunset/stars	Funnel
x Wiltschko et al., 1999	Australian silvereye	Spring	AUS	120° CCW	130° CCW***	Y/Y	Sunset/stars	Funnel
y Wiltschko et al., 2001	Australian silvereye	Spring	AUS	120° CCW	108° CCW***	Y/Y	Sunset/stars	Funnel
(z) Bäckman et al., 1997	Chaffinch	Autumn	SWE	90° CCW	84° CW/96° CCW	Y/Y	Sun	160°

Table continued on next page.

Table 2. *Continued*

	Reference	Species (age)	Season	Place	Shift	Response	Significance of control/ experiment	Celestial cue(s) available during calibration	View of sky around zenith
(B) Orientation of control/experimental group not significantly different from sunset and not in migratory direction									
a	Sandberg et al., 1988a,b	European robin (juv+ad)	Spring	SWE	90° CW	33° CCW*	Y^2/Y^2	Sunset/stars	90°
b	Sandberg et al., 1988a,b	European robin (juv+ad)	Autumn	SWE	90° CW	6° CW^{ns}	Y^2/Y^2	Sunset/stars	90°
c	Sandberg et al., 1988a,b	European robin (juv+ad)	Spring	SWE	90° CCW	9° CW^{ns}	Y^2/Y^2	Sunset/stars	90°
d	Sandberg et al., 1988a,b	European robin (juv+ad)	Autumn	SWE	90° CCW	16° CW^{ns}	Y^2/Y^2	Sunset/stars	90°
e	Sandberg et al., 1991	Northern wheatear (juv)	Autumn	SWE	90° CCW	38° CCW^{ns}	Y^2/Y^2	Sunset/stars	90°
f	Åkesson, 1994	Pied flycatcher (juv+ad)	Spring	SWE	90° CCW	8° CW^{ns}	Y^2/Y^2	Sunset/stars	160°
g	Åkesson, 1994	Thrush nightingale (juv+ad)	Spring	SWE	90° CCW	7° CW^{ns}	Y^2/Y^2	Sunset/stars	160°
h	Åkesson, 1994	Common redstart (juv+ad)	Spring	SWE	90° CCW	15° CW^{ns}	Y^2/Y^2	Sunset/stars	160°
i	Åkesson, 1994	Common redstart (juv)	Autumn	SWE	90° CCW	41° CW^{ns}	Y^2/Y^2	Sunset/stars	160°
j	Sandberg et al., 2000	Indigo bunting	Autumn	USA	90° CCW	28° CCW^{9,ns} d	Y^2/Y^2	Sunset/stars	160°
k	Sandberg et al., 2000	Grey catbird	Autumn	USA	90° CCW	11° CW^{9,ns} d	Y^2/Y^2	Sunset/stars	160°
(C) Control/experimental groups not significantly oriented									
a	Wiltschko et al., 1971	European robin	Autumn	DEU	115° CW	(146° CW)	N/Y	Sunset/stars/sunrise	⩽102°
b	Wiltschko and Höck, 1972	European robin	Spring	DEU	115° CW	(23° CCW)^{ns}	N/Y	Sunset/stars	⩽102°
c	Wiltschko and Höck, 1972	European robin	Autumn	DEU	115° CW	(16° CCW)^{ns}	N/Y	Sunset/stars	⩽102°
d	Wiltschko and Wiltschko, 1975a	Garden warbler	Autumn	ESP	120° CW	(152° CW)***	N/N	Sunset/stars/sunrise	95°
e	Wiltschko and Wiltschko, 1975a	Subalpine warbler	Autumn	ESP	120° CW	(145° CW)***	N/Y	Sunset/stars/sunrise	95°
f	Bingman and Wiltschko, 1988	Dunnock	Spring	DEU	120° CCW	(144° CW)***	Y/N	Sunset/stars	Funnel
g	Sandberg et al., 1991	Northern wheatear (juv)	Autumn	GRL	90° CCW	(8° CCW)^{ns}	Y^2/N	Sunset/stars	90°
h	Åkesson, 1993	Marsh warbler (juv)	Autumn	SWE	90° CCW	(57° CW)^{ns}	Y/N	Sunset/stars	160°
i	Åkesson, 1993	Marsh warbler (juv)	Autumn	KEN	90° CCW	(24° CW)^{ns}	Y/N	Sunset/stars	160°

In these studies, the birds were exposed to a shifted magnetic field under the natural sky during the experiment. In most studies the birds were exposed once to the cue conflict (exceptions: Ah–n, v–y and Cd,e, where single birds were tested several times).

d indicates experiments with a delayed shift.

Studies listed in parentheses were not included in the CW/CCW shift analysis, because the shift was not significant or the experiments were not carried out at sunset.

For further information see Table 1.

[1] Orientation not significantly different from sunset position, but into migratory direction.

[2] Orientation not significantly different from sunset position.

[3] Fat individuals.

[4] Years 1997–1999.

[5] Control direction NNW instead of NE.

[6] Calculated from experiments performed day 7 and later.

[7] During tidal window when birds normally depart.

[8] Mean shift.

[9] Delayed response to shift in release experiments (see Table 3).

Table 3. *Orientation studies examining the after effects to cue conflicts during migration*

	Reference	Species (age)	Season	Place	Magnetic field shift	Response	Significance of control/ experiment	Celestial cue(s) available during calibration	View of sky	Type of experiment	Magnetic compass recalibrated	Celestial compass recalibrated
(A) Both experimental and control groups significantly unimodally oriented, with controls oriented in the seasonally appropriate migratory direction												
a	Cochran et al., 2004	Grey-cheeked thrush	Spring	USA	ø77° CW	65° CCW***,[1]	Y/Y	Sunset	Full	Radio tracking	Y	
b	Cochran et al.. 2004	Swaison's thrush	Spring	USA	ø86° CW	79° CCW*,[1]	Y/Y	Sunset	Full	Radio tracking	Y	
c	Sandberg et al., 2000	Red-eyed vireo	Autumn	USA	90° CW	104° CW***	Y/Y	Sunset/stars	160°	Release		Y
d	Sandberg et al., 2000	Northern waterthrush	Autumn	USA	90° CW	113° CW***	Y/Y	Sunset/stars	160°	Release		Y
e	Wiltschko et al., 1998b	Australian silvereye	Spring	AUS	120° CW	103° CW***	Y/Y	Sunset/stars	Funnel	Vertical magnetic field		Y
f	Sandberg et al., 2000	Indigo bunting	Autumn	USA	90° CCW	121° CCW***	Y/Y	Sunset/stars	160°	Release		Y
g	Sandberg et al., 2000	Grey catbird	Autumn	USA	90° CCW	106° CCW***	Y/Y	Sunset/stars	160°	Release		Y
h	Åkesson et al., 2002	White-crowned sparrow (juv)	Autumn	CAN	90° CCW	87° CCW***	Y/Y	Sun	Full	Natural conditions		Y
i	Wiltschko et al., 1998b	Australian silvereye	Spring	AUS	120° CCW	135° CCW***	Y/Y	Sunset/stars	Funnel	Vertical magnetic field		Y
j	Wiltschko et al., 1999	Australian silvereye	Spring	AUS	120° CCW	135° CCW***	Y/Y	Sunset/stars	Funnel	Vertical magnetic field		Y
k	Wiltschko et al., 1999	Australian silvereye	Spring	AUS	120° CCW	0° $^{\mathrm{ns}}$	Y/Y	Sunset/stars	Funnel	Indoors	N	
l	Wiltschko et al., 2001	Australian silvereye	Spring	AUS	120° CCW	94° CCW***	Y/Y	Sunset/stars	Funnel	Vertical magnetic field		Y
(B) Direction of shift in orientation not discernible because of bimodal response(s)												
a	Able and Able, 1995a	Savannah sparrow (ad)	Autumn	USA	90° CW/CCW	91° Axial***	Y/Y	All	Full	Indoors	Y	
b	Able and Able, 1995a	Savannah sparrow (juv)	Autumn	USA	90° CW/CCW	101° Axial***	Y/Y	All	Full	Indoors	Y	
c	Bingman and Wiltschko, 1988	Dunnock	Spring	ITA	120° CW	104° CCW/76° CW***	Y/Y	Sunset/stars	Funnel	Vertical magnetic field		Y
(C) Control/experimental groups not significantly oriented												
a	Wiltschko and Wiltschko, 1975a	Garden warbler	Autumn	ESP	120° CW	(156° CW)	N/N	Sunset/stars/sunrise	95°	Vertical magnetic field		
b	Wiltschko and Wiltschko, 1975b	European robin	Spring	ESP	120° CW	(120° CW)*d	Y/N	Sunset/stars/sunrise	95°	Vertical magnetic field		
c	Bingman, 1987	European robin	Spring	ITA	120° CW	(140° CW**)	N/Y	Stars	160°	Vertical magnetic field		

For further information see Table 1.

[1] According to Tables S1 and S2 in supplemental online material provided by Cochran et al., 2004.

Table 4. *Summary of outcomes of cue-conflict experiments in relation to access to cues and view of sky*

	No view of horizon (90–160° view of sky from a funnel/octagonal registration cage)	Full view of sky (from cage)
Magnetic compass calibration	1 (1Be)	8 (1Ac,d; 1Ba,d; 3Aa,b; 3Ba,b)
No magnetic compass calibration	1 (3Ak)	1 (1Bc)
Celestial compass calibration	4 (3Ae,i,j,l) 1 (3Bc)	
No celestial compass calibration	0	2 (1Aa,b)
Shifted orientation in the direction of the magnetic field shift (consistent with recalibration of celestial, rather than magnetic, compass)	18 (2Ac–f,h–k,m,n,q–t,v–y) 4 (3Ac,d,f,g)	0
No shifted orientation	4 (2Aa,b,o,p)	0
Total	33	11

Numbers refer to the different studies as outlined in Tables 1–3. Included are all studies from Tables 1A,B, 2A, 3A,B. Only studies performed at sunset were included, since sample sizes for cue-conflict experiments carried out at sunrise (*N*=1: Table 2Ag), under the sun (*N*=3: Table 2Au,z and Table 3Ah) or stars only (*N*=2: Table 1Bb and Table 2Al), were too small and none of them pointed towards a magnetic compass calibration (for other selection criteria, see section on cue-conflict experiments).

to see a maximum of 90–102° around the zenith, as do the octagonal registration cages. Studies that did not explicitly give the view of sky in degrees and did not mention the presence of a shield surrounding the funnel, were categorized into the first group.

Ignoring season, birds that had a full view of sky during the cue-conflict exposure recalibrated their magnetic compass in 8 out of 9 studies (Table 4). Birds that did not have a view of the sunset cues down to the horizon (view limited to 95–160° centered around the zenith from a funnel or octagonal orientation cage) followed the shifted magnetic field and presumably recalibrated celestial compass cues (see studies with release experiments after cue-conflict exposure; Table 3A), or showed no magnetic compass calibration, in 28 out of 29 studies (Table 4). In only one of these 29 studies was there evidence of recalibration of the magnetic compass (Table 1Be). The four studies in which the surrounding shields restricted the view of the birds in the funnels to only 90° around the zenith showed no response whatsoever to the magnetic field shift (Sandberg et al., 1988a,b; Table 2Aa,b,o,p; see below).

It was previously argued that only one exposure to the cue conflict would lead to a dominance of magnetic cues, thus to a recalibration of the celestial compass(es), while repeated exposures to the cue conflict would lead to a dominance of celestial cues and to a recalibration of the magnetic compass (e.g. Wiltschko et al., 1997, 1998a; Wiltschko and Wiltschko, 1999). In 10 out of the 22 studies in Table 2A tested at sunset the birds were exposed multiple times to the cue conflict (Table 2Ah–k,m,n,v–y), without recalibrating the magnetic compass. Some of the early studies (Wiltschko et al., 1971; Wiltschko and Wiltschko, 1975a,b; Table 2Ah–k) even exposed the birds to the cue conflict repeatedly during both sunset and sunrise cues, but in octagonal orientation cages that shielded all but 95–102° of the sky, and did not observe recalibration of the magnetic compass.

General discussion

The results of our initial analyses were consistent with the conclusions of earlier reviews, which suggested that the relative saliency of celestial and magnetic cues differs during the premigratory and migratory periods (e.g. Wiltschko et al., 1997, 1998a; Wiltschko and Wiltschko, 1999). During the premigratory period, celestial cues provided the primary calibration reference; the magnetic compass was recalibrated when birds were exposed to a rotated magnetic field in the presence of natural celestial cues. In a majority of experiments carried out during migration, however, birds exposed to a rotated magnetic field during migration showed a corresponding shift in the direction of migratory orientation, indicating that they are giving precedence to magnetic cues, although the consistency of this response depended on the direction that the magnetic field was rotated (see further discussion below). When tested for after-effects under natural celestial cues in the absence of magnetic cues (vertical magnetic field), they maintain the shifted direction, suggesting that the celestial compass cues had been recalibrated relative to the magnetic field (Bingman and Wiltschko, 1988; Wiltschko et al., 1998b, 1999, 2001; Tables 3Ae,i,j,l,Bc).

Subsequent analyses suggested an alternative explanation for the differences in the response to the cue conflict. The response to the cue conflict during both the premigratory and migratory periods appears to be correlated with access to celestial cues during exposure to the cue conflict (Table 4). Birds exposed to the cue conflict during times of day that included sunset, recalibrated the magnetic compass if they had an unobstructed view including the region of sky near the horizon, regardless of whether they experienced the cue conflict during the premigratory (4 out of 5 experiments) or migratory (4 out of 4 experiments) season (Tables 1 and 3). In contrast, birds that were exposed to the cue conflict at times of day that did not include sunset or were prevented from seeing the region of sky near the horizon, did not recalibrate the magnetic compass, but instead relied on the magnetic field as the primary source of compass information and used the magnetic field to calibrate the remaining celestial compass cues. Thus, the integration of the multiple compass systems used by migratory birds may involve a much simpler and more invariant cue hierarchy than suggested by previous reviews (cf. Able, 1993; Wiltschko et al., 1997).

Importance of view of sky and cues at sunset/sunrise for magnetic compass calibration

Our analysis of cue-conflict experiments suggests that an unobstructed view of the sunset sky and, in particular, the region of sky near the horizon, is necessary for recalibration of the magnetic compass to occur. A number of studies suggest that polarized light patterns present at sunset (and, possibly also, sunrise) provide the reference information used to calibrate the magnetic compass. In contrast to controls, birds experiencing a shifted magnetic field under depolarizers that eliminated celestial polarized light cues, but permitted detection of both sun position and star patterns, did not show shifted orientation when subsequently tested with only magnetic field cues available (Able and Able, 1993). Able and Able (1995b) also showed that birds exposed to a shifted artificial polarization pattern at dusk and dawn in the ambient magnetic field, without seeing the sun or stars, recalibrated their magnetic compass according to the shifted polarization pattern. Exposure to an artificial polarized light pattern at sunset was also found to produce recalibration of the sun compass in a migratory bird (Phillips and Moore, 1992). Evidence from homing pigeons also suggests that sunrise (and possibly also sunset) polarized light cues from the region of sky near the horizon may be used as a compass calibration reference (Phillips and Waldvogel, 1988).

While there is considerable evidence for the role of cues available at sunset in calibrating other compass systems, the role of cues available at sunrise is less clear. Cue-conflict experiments by Sandberg et al. (2002) during sunrise showed results that were similar to their sunset results (the birds followed the magnetic compass), so sunrise factors alone, at least when the birds' view of the horizon sky is obstructed, do not provide the birds with the necessary information for magnetic compass recalibration. However, sunrise cues may be used as a calibration reference when birds have a full view of the sky down to the horizon, perhaps in combination with sunset cues (e.g. to provide an estimate of true geographic North; Phillips and Waldvogel, 1988), but no studies have been carried out yet to specifically address this possibility.

Interestingly, although birds tested in funnel experiments in which their view of the sky was restricted to between 95–160° centered around the zenith did not recalibrate the magnetic compass, they still responded to celestial polarized light cues at sunset (see references in Table 2 and Wiltschko and Wiltschko, 1974). In the absence of magnetic cues, birds tested with depolarizers covering the funnels were disoriented, whereas birds given an undisturbed view of the natural sky from orientation funnels showed seasonally appropriate orientation (Helbig, 1990, 1991). Thus, a subset of the available skylight polarization patterns appears to be used by migratory birds at sunset even when a view of the horizon sky is blocked. Interestingly, however, birds whose view of the sky was restricted even further (i.e. restricted to 90° centered around the zenith; Sandberg, 1988, 1991; Sandberg et al., 1988a,b) showed aberrant orientation and/or did not respond normally to the shifted magnetic field or polarization patterns. Instead they showed: (1) no reaction to rotation of the magnetic field (Table 2Aa,b,o,p), (2) non-migratory orientation that was not significantly different from the sunset azimuth (Table 2Ba–e and Sandberg, 1988, 1991), or (3) no response to an artificially shifted polarization pattern (Sandberg, 1988). Thus birds followed the shift in magnetic direction instead of recalibrating the magnetic compass, and recalibrated the available celestial compass cues with respect to the rotated magnetic cues, only when they had access to a view of sky in the funnel experiments that was ⩾95° but ⩽160°; Table 2, and see below).

Overall, these findings indicate (1) that access to the region of the sky immediately above the horizon is necessary for recalibration of the magnetic compass and (2) that access to a region of sky spanning at least 95° around the zenith appears to be necessary for the birds to be able to react to changes of the magnetic field (see below) or other celestial cues. These conclusions suggest that polarized light cues from the region of sky included in the view from 95° to 165° around the zenith, but not from the region of sky immediately around the zenith (i.e. within ±45°), functions differently (as a source of compass information) from those from the region of sky immediately above the horizon (as a compass calibration reference), as suggested by Phillips and Waldvogel (1988) for homing pigeons. And, secondly, that access to light from the celestial hemisphere may influence the birds' use of the light-dependent magnetic compass (see below).

The importance of sunset (and maybe also sunrise) cues for magnetic compass recalibration is further supported by two studies exposing birds to a full view of celestial cues down to the horizon that did not result in a magnetic compass recalibration. In both studies the cue-conflict exposure did not include sunset or sunrise.

Consistent with the conclusion that sunset (and possibly also sunrise) polarized light cues are necessary for recalibration of the magnetic compass, two studies found that exposure to a cue conflict with a full view of the sky did not result in recalibration of the magnetic compass, if the exposure did not include sunrise and sunset. In an experiment carried out during the premigratory season, Able and Able (1990b) exposed birds to the cue conflict only during the night, so that the birds could only use stars for calibration (Table 1Bb). Even though the birds were exposed to a full view of the starry sky in the shifted magnetic field, they did not recalibrate the magnetic compass. In an experiment carried out during migration, Åkesson et al. (2002) exposed birds to the cue conflict during the afternoon hours, thus the birds only had access to sun and other daytime polarized light cues and did not experience sunset cues during the exposure (Table 3Ah). When tested the same evening under natural conditions, the birds followed the magnetic field shift, thus had not recalibrated the magnetic compass. Although small in number, these studies support the theory that birds need a full view of celestial cues at sunset (or possibly sunrise) in order to recalibrate their magnetic compass.

If the birds given brief exposures to cue conflicts in Emlen funnels do not have access to celestial cues from the region of the sky near the horizon, but instead rely on the magnetic compass and use it to calibrate other celestial compass systems (see earlier discussion), what celestial cues are recalibrated relative to the magnetic field under these conditions? Clearly, other types of celestial cues must be involved, e.g. either star patterns or zenith polarized light patterns. Star patterns do not appear to be involved in recalibration of the magnetic compass. Experiments that exposed birds to a premigratory cue conflict between magnetic and stellar cues, by changing the direction of rotation of artificial star patterns, showed no calibration of the magnetic compass when the birds were tested with access to magnetic cues only (Wiltschko and Wiltschko, 1976; Beason, 1987; Weindler et al., 1998; but see Able and Able, 1990a). Instead, the magnetic compass seems to be involved in calibrating the star compass, which by itself only provides information about the deviation of the migratory direction away from the center of celestial rotation, to establish the population-specific migratory direction (Weindler et al., 1996, 1997). Therefore, we envision a cue hierarchy in which celestial cues available at sunset/sunrise (presumably polarized patterns from the region of sky near the horizon) provide the primary reference system for calibration of the magnetic compass, while the magnetic compass in turn is used to calibrate the star compasses, as well as zenith polarized light patterns. The magnetic compass may play a similar role in calibrating the sun compass for daytime orientation, as suggested for homing pigeons (Phillips and Waldvogel, 1988; but see Wiltschko et al., 1976, 1983, 1984; Wiltschko and Wiltschko, 1990).

Asymmetry in responses to CW and CCW shifts

Prinz and Wiltschko (1992) obtained evidence for an asymmetry in the response to premigratory exposure to shifted magnetic fields. They observed recalibration of the magnetic compass only when the magnetic field was shifted CCW/AS relative to the celestial cues. Their birds became disoriented when the field was shifted CW/WS. Unfortunately, in the only other studies involving cue conflicts during the premigratory period in which birds were exposed to a CW shift, the birds oriented bimodally (Able and Able, 1990b), making it impossible to determine the direction of the shift, or they were not tested to determine whether recalibration of the magnetic compass had occurred (experiments in a vertical magnetic field; Able and Able, 1997). Our analyses of cue-conflict experiments carried out during migration also provided evidence for an asymmetry in the response to different directions of rotation of the magnetic field. Birds exposed to CW shifts (and even more to WS shifts) of the magnetic field generally followed the shift with remarkable accuracy compared to birds exposed to CCW/AS shifts, which were more variable in their responses (see also Åkesson, 1994). Moreover, CCW/AS shifts were also disproportionately represented in experiments reporting a phototactic response toward sunset (rather than migratory orientation) in both control and experimental groups and in experiments that showed directed orientation in the control groups, but disorientation in the experimental group[§]. This asymmetry is analogous to the asymmetry reported by Prinz and Wiltschko (1992) during premigratory exposures, although they found the opposite tendency in the effects of the two treatments (i.e. a strong shift by birds exposed to a CC/AS shift and disorientation in birds exposed to a CW/WS shift).

One interesting possibility is that the asymmetry in the birds' responses to CW/WS and CCW/AS rotations of the magnetic field may be related in some way to the strong asymmetry in the role of the right and left eyes in mediating the light-dependent magnetic compass response of birds (Wiltschko et al., 2002). Evidence that the magnetic compass of birds is light dependent (Wiltschko et al., 1993) suggests that birds perceive the magnetic field as a pattern of light intensity and/or color, either superimposed on the normal visual input or processed by a separate (i.e. non-visual) photoreception system. For example, a recent theoretical model by Ritz et al. (2000) suggests that the biophysical process that underlies the light-dependent magnetic compass will cause a decrease in sensitivity to light in magnetically sensitive photoreceptors aligned either parallel or antiparallel to the axis of the magnetic field. If so, the magnetic field might be perceived as two darker areas (or areas of a particular color, if the magnetically sensitive receptors provide inputs to a color-opponent mechanism) superimposed on the visual field at either end of the magnetic field axis[¶] (see Fig. 6 in Ritz et al., 2000). In either case, the inclination of the magnetic field in the northern and southern temperate zones will cause this pattern to be 'tilted' at a steep angle, with one end of the pattern viewed against the sky and the other viewed against the substrate; in orientation

---

[§] In these studies, control and experimental tests of individual birds were alternated or the order randomized, so in a majority of control tests the birds had experienced the cue conflict at least once previously, which could explain why sunset attraction was observed in both the control and experimental groups.

[¶] Because the effect of the magnetic field on the mechanism proposed by Ritz et al. (2000) is independent of polarity, as is the avian magnetic compass (reviewed by Wiltschko and Wiltschko, 1995), the response of the light-dependent magnetic compass is predicted to be radially (= 'axially') symmetrical, i.e. the pattern of response produced at one end of the magnetic field axis will be identical to that produced at the other end of the magnetic field axis. This is consistent with the well-known observation that migratory birds use the inclination or dip-angle of the magnetic field to distinguish between the two ends of the magnetic axis and are unable to orient in a horizontal magnetic field (Wiltschko and Wiltschko, 1972).

studies, the lower end of the pattern will typically be viewed against the interior of an Emlen funnel or octagonal registration cage (cf. Fig. 2).

If birds only respond to the magnetic field in the upper (or lower) visual field, then the problem of the axial symmetry of the pattern is eliminated (see earlier discussion; Fig. 2). However, the lateralization of the avian magnetic compass could make perception of this pattern in only the upper (or lower) hemisphere strongly dependent on the horizontal alignment of the bird's head. This dependence might account for the tendency of birds to respond more readily to ~90° rotations of the magnetic field in one direction (e.g. CW), rather than the other (e.g. CCW), but only if birds tend to align their heads non-randomly with respect to absolute (i.e. geographic) coordinates. So, for example, if birds use celestial cues to preferentially align their heads toward a particular geographic direction (e.g. geographic North) when checking the magnetic compass, the dark area produced by the magnetic compass in the upper visual field would be more easily detected in alignments of the magnetic field that caused this portion of the pattern to fall in the visual field of the right (magnetically sensitive) eye, rather than in the visual field of the left (non-magnetically sensitive) eye. Because of the differences in the inclination of the magnetic field in the two hemispheres (inclined down to the north in the northern hemisphere and up to the north in the southern hemisphere; Fig. 2), the asymmetry in the birds' response to CW and CCW rotations of the magnetic field should be reversed (see below).

At present, there is no evidence that we know of to suggest that birds align themselves with respect to a geographically fixed reference, such as celestial light cues, when consulting the magnetic compass. However, the well-known asymmetry

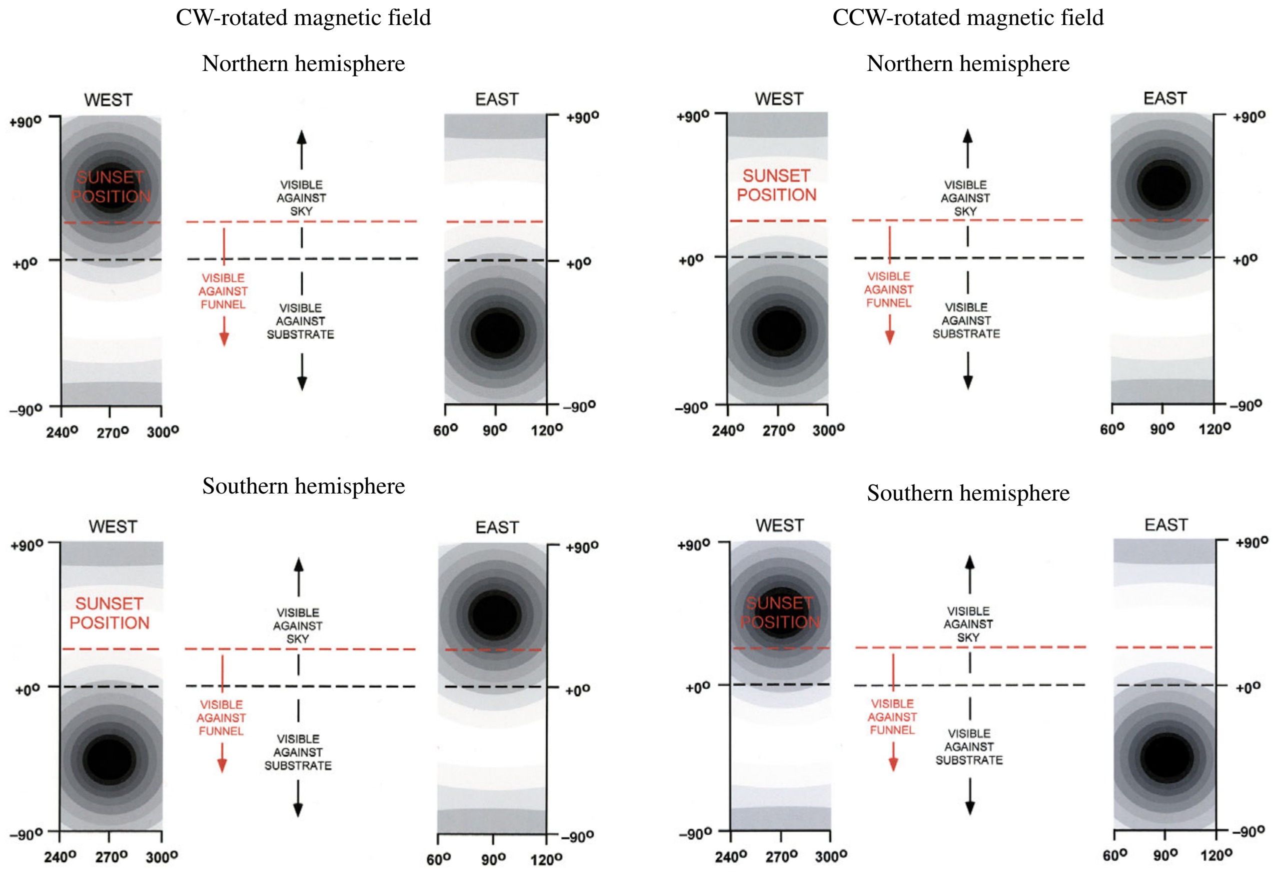

Fig. 2. Perception of the magnetic field as a visual pattern of light intensity and/or color (after Ritz et al., 2000). The inclination of the magnetic field in the northern (A) and southern (B) temperate zones will cause this pattern produced by the magnetic field to be 'tilted' at a steep angle, with one end of the pattern viewed against the sky and the other viewed against the substrate. Because of positive inclination in the northern and negative in the southern hemisphere, respectively, the upward end of the magnetic axis (where the portion of the pattern is visible against the sky) will be towards geographic South (gS) in the northern hemisphere, and towards gN in the southern hemisphere. Consequently, when the magnetic field is rotated 90° counterclockwise (CCW), the portion of the pattern viewed against the sky will be 90° clockwise (CW) of gN (east) in the northern hemisphere and 90° CCW of gN (west) in the southern hemisphere. Similarly, when the magnetic field is rotated 90° CW, the portion of the pattern viewed against the sky will be 90° CCW of gN (west) in the northern hemisphere and 90° CW of gN (east) in the southern hemisphere. Consequently, lateralization of the light-dependent magnetic compass in the right eye of birds (Wiltschko et al., 2002), or the gradients of light intensity and spectral content associated with the sky at sunrise or sunset, may cause differences in the response to CW and CCW shifts of the magnetic field (see text). In either case, any difference in the birds' response to CW and CCW shifts in experiments carried out in the northern hemisphere, should be reversed in the southern hemisphere (see text).

in the distribution of light intensity and spectral content of the evening sky may produce the same result. At sunset, there is a strong gradient in the intensity (brightest toward the sun) and spectral content (proportion of short wavelengths greatest away from the sun; McFarland and Munz, 1975) of natural skylight. If the magnetic field is perceived as a pattern of light intensity and/or color, and therefore is sensitive to the wavelength and intensity of light (as suggested by recent studies on the magnetic compass orientation of migratory birds; Wiltschko et al., 2000; Wiltschko and Wiltschko, 2001; Muheim et al., 2002), then a ~90° rotation of the magnetic field in one direction (e.g. CW) may result in a superposition of the magnetically derived pattern on the natural distribution of light intensity and color that makes the pattern more easily detectable, while the opposite rotation of the magnetic field (e.g. CCW) may result in the pattern being much less detectable (Fig. 2). The crucial point, however, is that the asymmetry in the birds' response to CW and CCW rotations of the magnetic field should be opposite in the northern and southern hemispheres. This is independent of whether the asymmetry in the response to CW and CCW rotations of the magnetic field is due to the lateralization of the magnetic compass and a tendency for birds to align themselves non-randomly when consulting the magnetic compass, or to the relationship of the light-dependent response of the magnetic compass to the rotated magnetic field and the natural distribution of light intensity and wavelength in the evening sky. Unfortunately, relatively few cue-conflict experiments under unmanipulated celestial cues have been carried out in the southern hemisphere, but nevertheless, data both from the cue-conflict experiments carried out during migration (see Tables 2 and 3), and from Prinz and Wiltschko's (1992) cue-conflict experiment carried out during the premigratory period, are compatible with this prediction, suggesting that further work is clearly justified.

Advantages of magnetic compass calibration during the premigratory and migratory periods

It has been previously suggested that there is a difference in the relative saliency of celestial and magnetic cues between the premigratory and migratory season. The magnetic compass was shown to be calibrated with respect to celestial cues during the premigratory season, but was suggested to act as the primary reference for calibration of other compass systems (including polarized light compasses) during migration. Able and Able (1996) found that recalibration of the magnetic compass in autumn was no longer evident in spring, which suggests that recalibration of the magnetic compass occurs prior to the onset of each migration. In addition, Weindler and Liepa (1999) showed that adult pied flycatchers recalibrate their magnetic compass when exposed to a cue conflict before the onset of migration, suggesting that calibration of the magnetic compass prior to migration occurs in adult, as well as juvenile, birds. As noted previously, however, the studies by Able and Able (1995a) and Cochran et al. (2004) that reported recalibration of the magnetic compass during the migratory season, suggest that magnetic compass calibration is not necessarily limited to the premigratory season.

Does it make sense that the magnetic compass would only be recalibrated before the start of the migratory journey and not during migration? Recalibration of the magnetic compass enables the birds to correct for differences in magnetic declination (i.e. the difference in the direction of the magnetic and geographic poles at a given location on the Earth's surface) that would otherwise cause a discrepancy between the directional information provided by the magnetic and celestial compasses. Therefore, calibrating the magnetic compass with respect to celestial cues before the onset of migration would eliminate the discrepancy between magnetic and celestial bearings in areas with large declinations (Able and Able, 1993, 1999). As a bird migrates to lower latitudes, changes in declination are less pronounced and the magnetic compass becomes more reliable, while at the same time, the course of the sun and the alignment of the polarized light pattern at sunset change with latitude, and star patterns learned during ontogeny are replaced by new configurations. This combination of factors has been suggested to explain why the magnetic compass appears to become the primary reference for maintenance of the migratory direction (and calibration of other cue systems) once migration is under way (reviewed by Alerstam, 1990; Muheim et al., 2003). Based on theoretical considerations, Alerstam (2001) concluded that it would not be efficient for bird migrants to follow magnetic loxodrome routes (constant magnetic courses) on the American continent, when the movement has a relatively strong east–west component. There, migrants following a constant magnetic course need to travel a longer distance than when following a geographic loxodrome (constant geographic route). In these cases, at least, repeated recalibrations of all of the compass systems, including the magnetic compass, with respect to a reference system that is tied to true geographic coordinates (e.g. celestial cues) would be adaptive. This, however, reverses on the European continent where strong east–west traveling migrants may travel shorter distances by following a magnetic loxodrome (Alerstam, 2001; Bingman et al., 2003). Therefore, regular recalibration of the magnetic compass may be a more efficient strategy on the American continent than in Europe and Asia. In conclusion, selection may have favored different orientation strategies in different regions of the world (Alerstam, 2001). It should be noted, however, that there are a number of alternatives to using the magnetic compass as a calibration reference during migration that would help to minimize the distance traveled by migratory species in Europe and Asia. Birds that use a single calibration reference derived from celestial cues both prior to and during migration could: (1) exhibit programmed change(s) in compass heading at appropriate points along the migration route (Gwinner and Wiltschko, 1978; Beck and Wiltschko, 1988; Helbig et al., 1989; Munro et al., 1993), or (2) exploit seasonal changes in celestial polarized light patterns at sunrise or sunset to produce adaptive deviations from the geographic loxodrome routes (i.e. more closely approximating magnetic loxodrome routes).

Conclusions

A large number of cue-conflict experiments have been performed over the last 35 years, and the aim of this review was to determine whether a reanalysis of the findings of these experiments, including those carried out during the past 5 years since the last comprehensive review of this literature, can provide any new insights into the integration of celestial and magnetic cues by migratory birds. Our findings suggest that accessibility to celestial (polarized light) cues at sunset from the region of sky immediately above the horizon can account for the differences in the response to the cue conflict observed between cue-conflict experiments carried out during the migratory season and those carried out prior to migration, rather than seasonal differences in the relative saliency of magnetic and celestial cues. If this interpretation is correct, the hierarchy of compass cues used by migratory birds may be much less plastic than previously thought. Based on these analyses, we propose that under natural conditions a single reference system is ultimately responsible for calibrating all of the compass systems of migratory birds. The proposed reference system involves polarized light cues visible at sunset from the region of sky near the horizon, as suggested previously for homing pigeons (Phillips and Waldvogel, 1988).

An interesting question for future research is whether sunset polarized light patterns alone are responsible for calibration of avian (or at least migratory bird) compass systems. A reference system based on sunset polarization patterns alone will shift considerably over the course of the year, due to the seasonal changes in the position of the setting sun. While in some instances a shifting compass course may be adaptive (see previous discussion) in cases where a fixed geographic loxodrome route is more efficient, averaging information from the polarization patterns present at sunrise and sunset can be used to derive an estimate of geographic north that is independent of time of year. An interesting question for future research, therefore, is whether polarized light cues present at sunrise play any role in the calibration of avian compass systems.

We want to thank Thomas Alerstam, Susanne Åkesson and Johan Bäckman and two anonymous referees for valuable comments on an earlier version of the manuscript. This study was supported by traveling fellowships by the Royal Physiographical Society in Lund, Sweden and the Journal of Experimental Biology, as well as the Swiss National Science Foundation (postdoctoral fellowship; all to R.M.), and by the National Science Foundation grant IBN04-25712 (to J.B.P.). Part of this study was financed by a grant from the Swedish Science Research Council (to S. Åkesson).

References

Able, K. P. (1982). Skylight polarization patterns at dusk influence migratory orientation in birds. *Nature* **299**, 550-551.

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

Able, K. P. and Able, M. A. (1990a). Calibration of the magnetic compass of a migratory bird by celestial rotation. *Nature* **347**, 378-380.

Able, K. P. and Able, M. A. (1990b). Ontogeny of migratory orientation in the Savannah sparrow, *Passerculus sandwichensis*: calibration of the magnetic compass. *Anim. Behav.* **39**, 905-913.

Able, K. P. and Able, M. A. (1993). Daytime calibration of magnetic orientation in a migratory bird requires a view of skylight polarization. *Nature* **364**, 523-525.

Able, K. P. and Able, M. A. (1995a). Interactions in the flexible orientation system of a migratory bird. *Nature* **375**, 230-232.

Able, K. P. and Able, M. A. (1995b). Manipulations of polarized skylight calibrate magnetic orientation in a migratory bird. *J. Comp. Physiol. A* **177**, 351-356.

Able, K. P. and Able, M. A. (1996). Migratory orientation: Autumn calibration of magnetic orientation is not evident in spring. *Naturwissenschaften* **83**, 517-518.

Able, K. P. and Able, M. A. (1997). Development of sunset orientation cues in a migratory bird: no calibration by the magnetic field. *Anim. Behav.* **53**, 363-368.

Able, K. P. and Able, M. A. (1999). Evidence for calibration of magnetic migratory orientation in Savannah sparrows reared in the field. *Proc. R. Soc. Lond. B* **266**, 1477-1481.

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., Morin, J., Muheim, R. and Ottosson, U. (2002). Avian orientation: effects of cue-conflict experiments with young migratory songbirds in the high Arctic. *Anim. Behav.* **64**, 469-475.

Alerstam, T. (1990). Ecological causes and consequences of bird orientation. *Experientia* **46**, 405-415.

Alerstam, T. (2001). Evaluation of long-distance orientation in birds on the basis of migration routes recorded by radar and satellite tracking. *J. Navig.* **54**, 393-403.

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.* London: Academic Press.

Beason, R. C. (1987). Interaction of visual and non-visual cues during migratory orientation by the bobolink, *Dolichonyx oryzivorus*. *J. Ornithol.* **128**, 317-324.

Beck, W. and Wiltschko, W. (1988). Magnetic factors control the migratory direction of pied flycatchers, *Ficedula hypoleuca.* In *Acta XIX Congress of International Ornithology* (ed. H. Quellet), pp. 1955-1962. Ottawa: University of Ottawa Press.

Berthold, P. (1991). Genetic control of migratory behaviour in birds. *Trends Ecol. Evol.* **6**, 254-257.

Berthold, P. (1996). *Control of Bird Migration.* London: Chapman and Hall.

Bingman, V. P. (1983). Magnetic field orientation of migratory Savannah sparrows with different first summer experience. *Behaviour* **87**, 43-51.

Bingman, V. P. (1984). Night sky orientation of migratory pied flycatchers raised in different magnetic fields. *Behav. Ecol. Sociobiol.* **15**, 77-80.

Bingman, V. P. (1987). Earth's magnetism and the nocturnal orientation of migratory European robins. *Auk* **104**, 523-525.

Bingman, V. P. and Wiltschko, W. (1988). Orientation of dunnocks, *Prunella modularis*, at sunset. *Ethology* **77**, 1-9.

Bingman, V. P., Budzynski, C. A. and Voggenhuber, A. (2003). Migratory systems as adaptive responses to spatial and temporal variability in orientation stimuli. In *Avian Migration* (ed. P. Berthold, E. Gwinner and E. Sonnenschein), pp. 457-469. Berlin, Heidelberg: Springer Verlag.

Cochran, W. W., Mouritsen, H. and Wikelski, M. (2004). Migrating songbirds recalibrate their magnetic compass daily from twilight cues. *Science* **304**, 405-408.

Emlen, S. T. (1975). The stellar orientation system of a migratory bird. *Sci. Am.* **233**, 102-111.

Emlen, S. T. and Emlen, J. T. (1966). A technique for recording orientation of captive birds. *Auk* **83**, 361-367.

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.

Gwinner, E. (1996). Circadian and circannual programmes in avian migration. *J. Exp. Biol.* **199**, 39-48.

Gwinner, E. and Wiltschko, W. (1978). Endogenously controlled changes in the migratory direction of garden warbler, *Sylvia borin*. *J. Comp. Physiol.* **125**, 267-273.

Helbig, A. J. (1990). Depolarization of natural skylight disrupts orientation of an avian nocturnal migrant. *Experientia* **46**, 755-758.

Helbig, A. J. (1991). Dusk orientation of migratory European robins, *Erithacus rubecula*: the role of sun-related directional information. *Anim. Behav.* **41**, 313-322.

Helbig, A. J., Berthold, P. and Wiltschko, W. (1989). Migratory orientation of blackcaps, *Sylvia atricapilla*: Population-specific shifts of direction during the autumn. *Ethology* **82**, 307-315.

McFarland, W. N. and Munz, F. W. (1975). The visible spectrum during twilight and its implications to vision. In *Light as an Ecological Factor: II* (ed. G. C. Evans, R. Bainbridge and O. Rackham), pp. 249-270. Oxford: Blackwell Scientific Publication.

Moore, F. R. (1987). Sunset and the orientation behaviour of migrating birds. *Biol. Rev.* **62**, 65-86.

Moore, F. R. and Phillips, J. B. (1988). Sunset, skylight polarization and the migratory orientation of yellow-rumped warblers, *Dendroica coronata*. *Anim. Behav.* **36**, 1770-1778.

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., Åkesson, S. and Alerstam, T. (2003). Compass orientation and possible migration routes of passerine birds at high arctic latitudes. *Oikos* **103**, 341-349.

Munro, U., Wiltschko, W. and Ford, H. (1993). Changes in the migratory direction of yellow-faced honeyeaters, *Lichenostomus chrysops*, during autumn migration. *Emu* **93**, 59-62.

Phillips, J. B. and Moore, F. R. (1992). Calibration of the sun compass by sunset polarized light patterns in a migratory bird. *Behav. Ecol. Sociobiol.* **31**, 189-193.

Phillips, J. B. and Waldvogel, J. A. (1988). Celestial polarized patterns as a calibration reference for sun compass of homing pigeons. *J. Theor. Biol.* **131**, 55-67.

Prinz, K. and Wiltschko, W. (1992). Migratory orientation of pied flycatchers: interaction of stellar and magnetic information during ontogeny. *Anim. Behav.* **44**, 539-545.

Ritz, T., Adem, S. and Schulten, K. (2000). A model for photoreceptor-based magnetoreception in birds. *Biophys. J.* **78**, 707-718.

Sandberg, R. (1988). Skylight polarisation does not affect the migratory orientation of European robins. *Condor* **90**, 267-270.

Sandberg, R. (1991). Sunset orientation of robins, *Erithacus rubecula*, with different fields of sky vision. *Behav. Ecol. Sociobiol.* **28**, 77-83.

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 bunting, *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. (1988a). Shifted magnetic fields lead to deflected and axial orientation of migrating robins, *Erithacus rubecula*, at sunset. *Anim. Behav.* **36**, 877-887.

Sandberg, R., Pettersson, J. and Alerstam, T. (1988b). 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., Moore, F. R. and Löhmus, M. (2000). Magnetic information calibrates celestial cues during migration. *Anim. Behav.* **60**, 453-462.

Sandberg, R., Moore, F. R., Bäckman, J. and 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.

Sauer, E. G. F. (1957). Die Sternenorientierung nächtlich ziehender Grasmücken, *Sylvia atricapilla*, *borin* and *curruca*. *Z. Tierpsychol.* **14**, 20-70.

Schmidt-Koenig, K. (1990). The sun compass. *Experientia* **46**, 336-342.

Weindler, P. and Liepa, V. (1999). The influence of premigratory experience on the migratory orientation of birds. In *Proceedings of the 22nd International Ornithology Congress* (ed. N. J. Adams and R. H. Slotow), pp. 979-987. Johannesburg: BirdLife South Africa.

Weindler, P., Wiltschko, R. and Wiltschko, W. (1996). Magnetic information affects the stellar orientation of young bird migrants. *Nature* **383**, 158-160.

Weindler, P., Baumetz, M. and Wiltschko, W. (1997). The direction of celestial rotation influences the development of stellar orientation in young garden warblers, *Sylvia borin*. *J. Exp. Biol.* **200**, 2107-2113.

Weindler, P., Liepa, V. and Wiltschko, W. (1998). The direction of celestial rotation affects the development of migratory orientation in pied flycatcher, *Ficedula hypoleuca*. *Ethology* **104**, 905-915.

Wiltschko, R. and Wiltschko, W. (1990). Zur Entwicklung der Sonnenkompassorientierung bei jungen Brieftauben. *J. Ornithol.* **131**, 1-19.

Wiltschko, R. and Wiltschko, W. (1995). *Magnetic Orientation in Animals.* Berlin: Springer.

Wiltschko, R. and Wiltschko, W. (1999). Celestial and magnetic cues in experimental conflict. In *Proceedings of the 22nd International Ornithology Congress* (ed. N. J. Adams and R. H. Slotow), pp. 988-1004. Johannesburg: BirdLife South Africa.

Wiltschko, R., Wiltschko, W. and Munro, U. (1997). Migratory orientation in birds: the effects and after-effects of exposure to conflicting celestial and magnetic cues. In *Orientation and Navigation – Birds, Humans and other Animals*, pp. 6.1-6.14. Oxford: Royal Institute of Navigation.

Wiltschko, R., Munro, U., Ford, H. and Wiltschko, W. (1999). After-effects of exposure to conflicting celestial and magnetic cues at sunset in migratory silvereyes, *Zosterops l. lateralis*. *J. Avian Biol.* **30**, 56-62.

Wiltschko, R., Munro, U., Ford, H. and Wiltschko, W. (2001). Orientation in migratory birds: time-associated relearning of celestial cues. *Anim. Behav.* **62**, 245-250.

Wiltschko, W. and Höck, H. (1972). Orientation behaviour of night-migrating birds (European robins) during late afternoon and early morning hours. *Wilson Bull.* **84**, 149-163.

Wiltschko, W. and Wiltschko, R. (1972). Magnetic compass of European robins. *Science* **176**, 62-64.

Wiltschko, W. and Wiltschko, R. (1974). Bird orientation under different sky sectors. *Z. Tierpsychol.* **35**, 536-542.

Wiltschko, W. and Wiltschko, R. (1975a). The integration of stars and magnetic field in the orientation system of night migrating birds. I. Autumn experiments with European warblers (Gen. *Sylvia*). *Z. Tierpsychol.* **37**, 337-355.

Wiltschko, W. and Wiltschko, R. (1975b). The integration of stars and magnetic field in the orientation system of night migrating birds. II. Spring experiments with European robins, *Erithacus rubecula*. *Z. Tierpsychol.* **39**, 265-282.

Wiltschko, W. and Wiltschko, R. (1976). Interrelation of magnetic compass and star orientation in night-migrating birds. *J. Comp. Physiol. A* **109**, 91-99.

Wiltschko, W. and Wiltschko, R. (2001). Light-dependent magnetoreception in birds: the behaviour of European robins, *Erithacus rubecula*, under monochromatic light of various wavelengths and intensities. *J. Exp. Biol.* **204**, 3295-3302.

Wiltschko, W., Höck, H. and Merkel, F. W. (1971). Outdoor experiments with migratory European robins in artificial magnetic fields. *Z. Tierpsychol.* **29**, 409-415.

Wiltschko, W., Wiltschko, R. and Keeton, W. T. (1976). Effects of a 'permanent' clock-shift on the orientation of young homing pigeons. *Behav. Ecol. Sociobiol.* **1**, 229-243.

Wiltschko, W., Wiltschko, R., Keeton, W. T. and Madden, R. (1983). Growing up in an altered magnetic field affects the initial orientation of young homing pigeons. *Behav. Ecol. Sociobiol.* **12**, 135-142.

Wiltschko, W., Wiltschko, R. and Keeton, W. T. (1984). The effect of a 'permanent' clock-shift on the orientation of experienced homing pigeons. *Behav. Ecol. Sociobiol.* **15**, 263-272.

Wiltschko, W., Munro, U., Ford, H. and Wiltschko, R. (1993). Red light disrupts magnetic orientation of migratory birds. *Nature* **364**, 525-527.

Wiltschko, W., Weindler, P. and Wiltschko, R. (1998a). Interaction of magnetic and celestial cues in the migratory orientation of passerines. *J. Avian Biol.* **29**, 606-617.

Wiltschko, W., Wiltschko, R., Munro, U. and Ford, H. (1998b). Magnetic versus celestial cues: cue-conflict experiments with migrating silvereyes at dusk. *J. Comp. Physiol. A* **182**, 521-529.

Wiltschko, W., Wiltschko, R. and Munro, U. (2000). Light-dependent magnetoreception in birds: does directional information change with light intensity? *Naturwissenschaften* **87**, 36-40.

Wiltschko, W., Traudt, J., Güntürkün, O., Prior, H. and Wiltschko, R. (2002). Lateralization of magnetic compass orientation in a migratory bird. *Nature* **419**, 467-470.