

Shifted magnetic fields lead to deflected and axial orientation of migrating robins, *Erithacus rubecula*, at sunset

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Abstract. The migratory orientation of the robin was tested in shifted magnetic fields during the twilight period after sunset, under clear skies and under simulated total overcast. The horizontal direction of the geomagnetic field was shifted 90° to the right or left in relation to the local magnetic field, without changing either the intensity of the field or its angle of inclination. Experiments were conducted during both spring and autumn, with robins captured as passage migrants at the Falsterbo and Ottenby bird observatories in southern Sweden as test subjects. Generally, the orientation of robins was affected by magnetic shifts compared to controls tested in the natural geomagnetic field. Autumn birds from the two capture sites differed in their responses, probably because of different migratory dispositions and body conditions. The robins most often changed their orientation to maintain their typical axis of migration relative to the shifted magnetic fields. However, preferred directions in relation to the shifted magnetic fields were frequently reverse from normal, or axial rather than unimodal. These results disagree with suggested mechanisms for orientation by visual sunset cues and with the proposed basis of magnetic orientation. They do, however, demonstrate that the geomagnetic field is involved in the sunset orientation of robins, probably in combination with additional visual or non-visual cues that contribute to establish magnetic polarity.

The robin, *Erithacus rubecula*, a common night migrant in Europe, has become a classic experimental subject in orientation research. It was the first bird species for which a compass sense based on the geomagnetic field was demonstrated (Merkel & Wiltschko 1965; Wiltschko 1968; Wiltschko & Wiltschko 1972). Further experiments examined the relative importance of magnetic and stellar cues in the orientation system of robins. The results indicate a primary importance of the magnetic compass for selection of a seasonally appropriate migratory direction, whereas the star compass assumes a secondary role onto which the preselected direction can be transferred for maintenance and accuracy of the orientation (Wiltschko et al. 1971; W. Wiltschko & R. Wiltschko 1974, 1975, 1976; R. Wiltschko & W. Wiltschko 1978). According to experiments during the spring in Spain, robins tested under clear starry skies responded to shifted magnetic fields only after repeated tests. This suggests that they rely on the star compass during extended time intervals between successive calibrations in relation to the magnetic compass (Wiltschko & Wiltschko 1975). No such delay in responses to shifted magnetic fields was noted in tests under natural night skies in Germany, but the

sky was often partly or completely overcast during these experiments (Wiltschko et al. 1971). Additional data concerning the influence of the Earth's magnetic field and of displacements on the orientation of robins have been reported by Rabøl (1975, 1979, 1981).

In a series of experiments with savannah sparrows, *Passerculus sandwichensis*, in North America, Moore (1978, 1980, 1982, 1985) drew attention to the importance of sunset cues during the twilight period for the orientation of this nocturnal migrant. Radar studies have shown that nocturnal passerine migrants normally depart during twilight (Alerstam 1976; Richardson 1978), a fact that points to the particular relevance of orientation cues available at that time (Vleugel 1953; Emlen 1980). By manipulating the direction towards sunset in a mirror experiment, Moore (1982) was able to demonstrate that a deflection of this cue caused a corresponding shift in the orientation of savannah sparrows. Furthermore, by altering the position of the setting sun experimentally and simultaneously changing the direction of magnetic north to the opposite direction, Moore (1985) showed that savannah sparrows primarily orient in relation to the sunset azimuth and not according to

the geomagnetic field. The importance of celestial cues during the sunset period has been suggested for other species as well, like the white-throated sparrow *Zonotrichia albicollis* (Emlen & Demong 1978; Bingman & Able 1979; Able 1982 a, b; Able & Cherry 1986), and recently for the robin by Katz (1985).

Is the geomagnetic field of primary importance for the sunset orientation of robins, as it seems to be during nocturnal darkness and in visually cue-less situations? Or, are visual sunset cues of primary importance, so that robins will fail to respond to artificially shifted magnetic fields like savannah sparrows and other North American emberizines do? To answer these questions and to investigate the relative importance of magnetic and celestial cues for the orientation of robins at the normal departure time for their migratory flights, i.e. during twilight after sunset, we carried out orientation experiments with this species in artificially shifted magnetic fields during spring and autumn migration.

Migrating robins captured at two nearby stop-over sites in southern Sweden (the Falsterbo and Ottenby bird observatories) showed significantly different sunset orientation, probably as a result of differences in the birds' body condition and in their migratory situation with respect to impending and preceding flights over land and sea, respectively (Sandberg et al. 1988). In this study, we used exactly the same test procedure at the two sites. This enabled us to determine whether the relative importance of visual and magnetic cues in the sunset orientation of robins depends on different migratory dispositions.

METHODS

Test Birds and Equipment

Migrating robins captured at Falsterbo Bird Observatory (55° 23'N, 12° 50'E) were transported by car approximately 55 km to the northeast, to a test site at the ecological field station Stensoffa (55° 42'N, 13° 25'E), in the vicinity of Lund. Orientation experiments with artificially shifted magnetic fields were conducted at Stensoffa during the spring migration period (April and May) in 1984 and 1985, and during the autumn migration period (September and October) in 1985. Robins captured at Ottenby Bird Observatory (56° 12'N, 16° 24'E) were taken by car to a nearby test site, only 3 km to

the north, where the corresponding experiments were performed during spring migration in 1986 and the autumn passage in 1984 and 1986. At the test sites, each bird was kept in captivity on average 2 weeks, during which time up to six orientation experiments under different conditions (see below) were performed.

Handling of birds as well as experimental equipment (non-magnetic materials), set-up and procedure were exactly the same at the two test sites, as described in the preceding paper (Sandberg et al. 1988). Orientation was recorded in modified 'Emlen-funnels' with automatic counter registrations of the activity in each 45° sector. The orientation cages were placed inside large plastic tubes, restricting the birds' view of the sky above to a sector of approximately 90° centred around the zenith (see Fig. 1 in Sandberg et al. 1988).

Magnetic coils were designed with a quadratic cross-section (800 × 800 mm) and with a 630 mm clearance between the coils in a pair. Each pair of coils was mounted on the outside surface of the screening tubes in order to hide them from the birds' view. Coil formers were made of reinforced plastic and wound with 200 turns of insulated copper wire with 0.6 mm diameter. The power supply was a 12-V car battery and the current was held constant at 6 V by a regulator. A pair of coils generated a horizontal magnetic field with an intensity $\sqrt{2} = 1.41$ times the horizontal intensity of the local geomagnetic field. By orienting such a pair of coils along an axis southeast/northwest or southwest/northeast, magnetic north could be deflected 90° to the right (to geographical east) or 90° to the left (to geographical west), respectively, without changing the total intensity or inclination of the magnetic field. For the area in the orientation cage to which the test birds effectively had access (within 100 mm radius from the centre, see Sandberg et al. 1988), the calculated homogeneity of the artificial horizontal magnetic field was 3% or less along the coil axis and 2% or less perpendicular to this axis (the corresponding homogeneity at the periphery of the cage was 7% or less and 5% or less, respectively). The $\pm 90^\circ$ deflections in magnetic horizontal directions were carefully checked by a magnetic compass needle when the coils were activated prior to each test. We used four pairs of coils, and during each test night two of them were oriented to shift magnetic north $+90^\circ$ relative to normal and the other two to obtain corresponding -90° shifts. The same coils were used in different

seasons at Falsterbo and Ottenby, respectively.

The local horizontal and vertical intensities of the geomagnetic field are approximately $17 \mu\text{T}$ and $46 \mu\text{T}$, respectively, with an angle of inclination at 70° . As pointed out above, these magnetic parameters remained unaltered in the artificially shifted magnetic fields.

Experimental Conditions

All tests took place outdoors, and test birds were installed in the experimental situation about 30 min before local sunset (Sandberg et al. 1988). The orientation was recorded during 1 h, starting 10 min after sunset. Robins were exposed to six different experimental conditions, with each individual tested only once per condition.

(1) Tests under clear skies (less than 5/8th cloud cover) with skylight from the setting sun clearly visible: (i) unmanipulated controls, (ii) magnetic north shifted $+90^\circ$ (mN $+90^\circ$) and (iii) magnetic north shifted -90° (mN -90°).

(2) Tests under simulated total overcast. To simulate overcast, a panel of 3 mm opaque diffusing Plexiglas was placed on top of the screening tube, thus preventing the test birds from seeing any celestial cues: (i) unmanipulated controls, (ii) magnetic north shifted $+90^\circ$ and (iii) magnetic north shifted -90° .

The results of the control tests are given in Sandberg et al. (1988). Control categories contain a larger number of tests because of the limited number of magnetic coils available for deflection experiments. Among the control data, we also incorporated tests carried out during seasons when no simultaneous experiments with shifted magnetic fields were performed. Including these data does not affect our conclusions, and there were no significant differences in orientation between years for different experimental categories. The sequential order between tests under the experimental conditions described above were highly variable among individuals.

Statistical Evaluation

On the basis of counter registrations from the orientation cages, a mean heading was determined by vector calculation for each individual and test. Bird-hours with fewer than 40 counter registrations or a highly scattered and unreliable orientation

($P > 0.05$ according to the Rayleigh test, Batschelet 1981) were excluded from analysis (Sandberg et al. 1988).

Individual mean headings were used to calculate second-order mean vectors and axes of orientation for each experimental condition according to Batschelet (1981). A mean axis of orientation was used when the vector length calculated from double angles (r_2) was larger than the mean vector length (r) of the unimodal mean vector. The Rayleigh test was applied to determine significant directional preferences. Scatter in orientation was compared between different samples by the 'test for the homogeneity of concentration parameters' (Mardia 1972). Differences in mean angles of orientation between experimental categories were investigated by using Mardia's (1972) one-way classification test. The latter test allows comparisons of mean angles between two samples with even moderate mean vector lengths, as long as the vector lengths do not differ significantly from each other. Furthermore, paired tests were also used to compare orientation under two different experimental conditions, i.e. the angular differences between each individual's mean heading under the two conditions were calculated. A difference in orientation at the individual level between two conditions is indicated if the resulting mean direction deviates significantly from 0° (confidence intervals were determined according to Batschelet 1981).

RESULTS

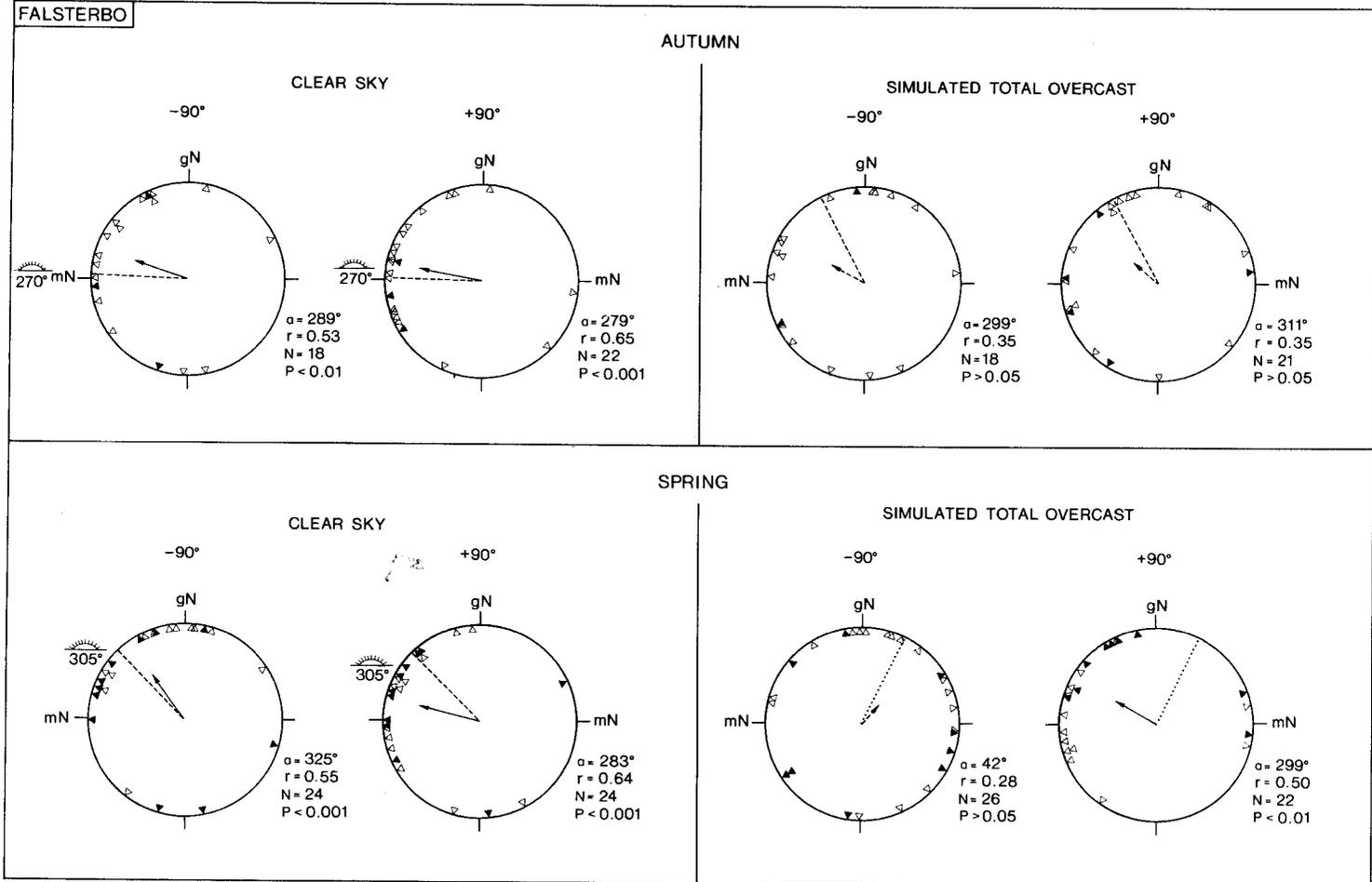
Orientation by Falsterbo Robins

Autumn

The Falsterbo robins maintained a westerly orientation under clear skies, approximately towards the sunset azimuth, irrespective of shifts in the magnetic field (Fig. 1). Under simulated overcast the orientation was too scattered to be significantly different from random ($P > 0.05$) with both deflections of magnetic north. Although these scattered data do not allow any conclusion concerning magnetic influences on overcast orientation, it seems unlikely that there is a marked deflection in relation to controls.

Spring

Under clear skies, there was no significant



difference between the mean directions of control and mN -90° tests. However, the orientation with mN $+90^\circ$ differed significantly from the control direction ($P < 0.05$, Mardia 1972). This divergence is also apparent from a one-sample paired analysis based on the angular difference between mean headings for each individual tested under the two conditions. According to this analysis, the robins showed a mean deflection in orientation of 41° (95% confidence interval = $\pm 32^\circ$) to the left under mN $+90^\circ$ in comparison with controls. This effect is surprising and means that the birds adopted a southerly orientation relative to the shifted magnetic field (Fig. 1).

Tests performed under simulated total overcast resulted in a statistically insignificant mean orientation of Falsterbo robins in the normal geomagnetic field towards north-northeast ($\alpha = 26^\circ$, $r = 0.23$, $N = 41$, $P > 0.05$, cf. Sandberg et al. 1988). A similar situation appeared with mN -90° , when again the orientation did not differ significantly from random. In contrast, with mN $+90^\circ$ the robins showed a fairly well-defined orientation towards geographical west-northwest, corresponding to magnetic south-southwest. One may note that under this latter condition a few individuals oriented away from the mean direction, indicating the possibility of a bimodal orientation. In fact, the mean axis of orientation ($\alpha = 285^\circ - 105^\circ$, $r_2 = 0.44$) is statistically significant ($P < 0.05$), although the unimodal mean vector, as shown in Fig. 1, gives a slightly better fit to the data.

Figure 1. Effects of artificial magnetic shifts on the orientation of robins captured at Falsterbo. Experiments were performed during both autumn and spring, under clear skies and simulated overcast, respectively. The mean azimuth of the setting sun 40 min after sunset (i.e. in the middle of the test hour) is indicated for the clear sky tests. A broken line is inserted in each circular diagram depicting the orientation of controls in the natural geomagnetic field (cf. Sandberg et al. 1988). When control orientation failed to reach significance, this line is substituted with a dotted line. Magnetic north (mN) was deflected -90° and $+90^\circ$ in relation to geographical north (gN). Each symbol represents a mean heading of an individual. Open symbols denote birds in their first year and closed symbols correspond to older birds. Only one test per individual is included for each experimental condition. The mean vector (α) of each sample is illustrated by an arrow whose length (r) is drawn relative to the radius of the circle = 1. All significance levels are according to the Rayleigh test.

Orientation by Ottenby Robins

Autumn

The shifted magnetic fields had a profound effect on the preferred directions of robins from Ottenby, leading to a bimodal pattern of orientation along an axis aligned approximately east/west (i.e. magnetically north/south) for all four categories of mN -90° and mN $+90^\circ$ experiments under clear and overcast skies, respectively (Fig. 2). In all of these four test conditions with shifted magnetic fields, the degree of scatter for axial orientation as signified by r_2 is considerably less than for the corresponding unimodal orientation as indicated by the vector length r (r_2/r in the four categories are 0.33/0.18, 0.43/0.31, 0.56/0.26 and 0.41/0.26), and three of the four unimodal mean vectors fail to reach significance. This is in dramatic contrast to the outcome of control experiments which showed highly significant unimodal orientation but no tendencies of bimodality (r_2/r in control tests under clear skies and simulated overcast are 0.06/0.39 and 0.13/0.37, respectively, Sandberg et al. 1988).

There is a significant difference between the four experimental categories in the relative number of birds that oriented in the two opposite modal sectors (roughly towards geographical east and west, respectively) along the mean axis of orientation (Table I, $\chi^2 = 9.3$, $df = 3$, $P < 0.05$). Most birds oriented in the modal sector towards geographical west under clear skies and in the east sector under simulated overcast. However, the observed number of headings in the two opposite modal sectors differ significantly from an equal probability distribution only for mN $+90^\circ$ tests under clear skies ($P < 0.05$, two-tailed binomial test).

There is no indication that individual birds oriented consistently in one of the two modal sectors, in relation to either the geographical or the magnetic compass direction. Table II shows that individuals heading in one modal sector with a shifted magnetic field may maintain this orientation or change it to the opposite sector when tested in the reverse magnetic field, without any significant consistency in directional choice along the mean axis of orientation ($P > 0.1$, Fisher exact probability tests).

Furthermore, there are no grounds for suspecting that the bimodality in the robins' orientation is due to lasting influences from preceding tests with shifted magnetic fields (cf. Wiltschko & Wiltschko

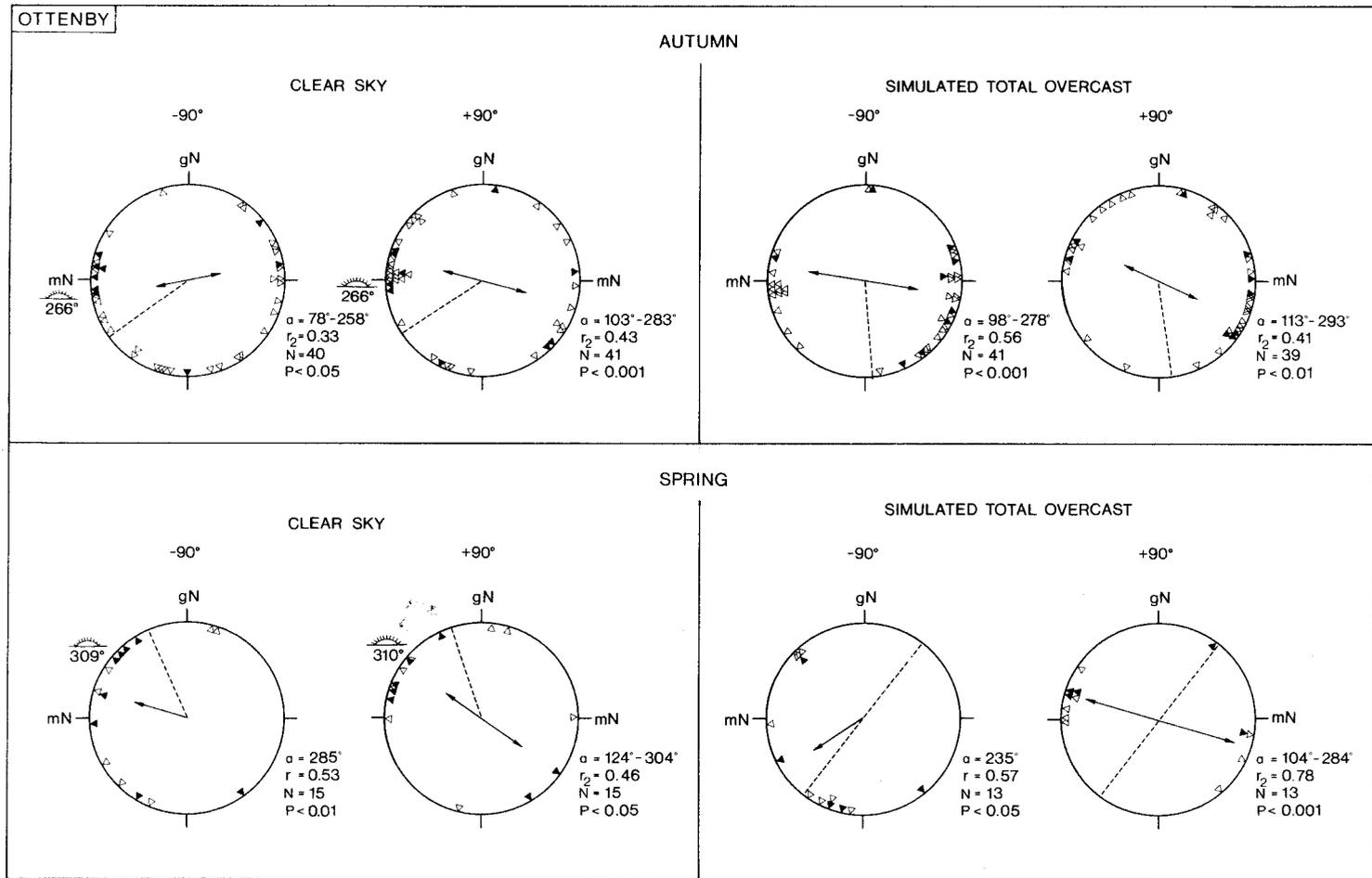


Figure 2. The orientation of robins, captured at Ottenby, in shifted magnetic fields during autumn and spring, respectively, under both clear skies and simulated overcast. The mean unimodal or, in cases where a mean axis of orientation provides a better fit to the data, bimodal vector (α) is shown in each circular diagram. For further explanations, see Fig. 1.

Table I. Number of individual headings in the two modal sectors, towards geographical west and east, $\pm 40^\circ$ along the mean axis of orientation

Experimental category	No. (%) of individual headings	
	In west modal sector	In east modal sector
Clear sky		
mN -90°	13 (54%)	11 (46%)
mN $+90^\circ$	21 (70%)	9 (30%)
Overcast		
mN -90°	12 (38%)	20 (62%)
mN $+90^\circ$	10 (36%)	18 (64%)

Four experimental categories of Ottenby robins exposed to shifted magnetic fields during autumn, are compared (cf. Fig. 2).

Table II. Relationship between mean headings of individual robins in experiments with the magnetic field shifted -90° and $+90^\circ$

mN $+90^\circ$	mN -90°	
	West modal sector	East modal sector
Clear skies		
West modal sector	6	5
East modal sector	0	4
Overcast		
West modal sector	4	5
East modal sector	4	7

The data refer to autumn orientation tests at Ottenby, under clear skies and simulated total overcast, respectively. The table shows the number of individuals with mean headings in the west and east (geographically) modal sectors $\pm 40^\circ$ along the mean axis of orientation, under the two conditions of magnetic shifts, respectively (cf. Fig. 2).

1975). When we restricted the analysis to the first test with a shifted magnetic field for each individual, preceded only by control tests in the normal geomagnetic field or with no preceding tests at all, axial orientation still remained evident. Hence, under overcast the mean axis of orientation is statistically significant for both mN $+90^\circ$ first-tests ($\alpha=114^\circ-294^\circ$, $r_2=0.42$, $N=17$, $P<0.05$) and mN -90° first-tests ($\alpha=92^\circ-272^\circ$, $r_2=0.64$,

$N=10$, $P<0.05$), while in both these cases significant unidirectionality failed to emerge ($r=0.20$ and 0.32 , $P>0.05$, respectively). Also for the mN $+90^\circ$ tests under clear skies, axial ($\alpha=104^\circ-284^\circ$, $r_2=0.30$, $N=16$, $P>0.05$) rather than unimodal orientation ($r=0.06$) is indicated, although the results fall short of significance. The number of first tests with mN -90° under clear skies are too few, $N=4$, to permit a meaningful analysis.

Spring

Ottenby robins generally responded to the shifted magnetic fields by orienting in geographically westerly directions, irrespective of whether the field was deflected $+90^\circ$ or -90° (Fig. 2). However, with mN $+90^\circ$ a few individuals preferred the opposite easterly direction, giving as a result an overall axial orientation. The experimental outcome in three of the four categories with shifted magnetic fields differed significantly from the corresponding control orientation ($P<0.05$, two-sample or paired tests). Only tests with mN $+90^\circ$ under clear skies did not deviate significantly from the control tests.

Orientation of Adults and Juveniles

In Figs 1 and 2 robins in their first year, i.e. on their first autumn or spring migration, are distinguished from older individuals. There are no indications of age-related differences in the orientation of the four experimental categories. Unfortunately, the number of old individuals is too small to permit a more detailed comparison of orientation performance between age groups.

DISCUSSION

Our results do not agree with suggested mechanisms for orientation by solar cues (Moore 1980, 1982, 1985; Able 1982a; Katz 1985) nor with the proposed basis of magnetic orientation (Wiltschko & Wiltschko 1972; Kiepenheuer 1984). A number of conclusions can be drawn from these unexpected results.

Response to Shifted Magnetic Fields

Except for the Falsterbo birds in autumn, the orientation of the robins under clear sunset skies was affected by imposed shifts in the magnetic field.

This is in contrast to the evidence presented for nocturnally migrating sparrows in North America, where attempts to detect any involvement of the magnetic compass in sunset orientation by experiments with shifted magnetic fields have failed to reveal any effects (Moore 1985; Able & Cherry 1986). However, Bingman (1983a) found that the sunset orientation of migratory naive savannah sparrows became disrupted in a non-directional vertical magnetic field.

The robins seem to respond immediately to the shifted magnetic fields, and there are no indications of a delay in the calibration between magnetic and visual compass cues as reported by Wiltschko & Wiltschko (1975) for robins tested under starry night skies (but see Wiltschko et al. 1971).

Differences Between Falsterbo and Ottenby Robins

The differences in orientation between robins captured at Falsterbo and Ottenby, and especially the lack of significant directional responses to shifted magnetic fields by autumn robins from Falsterbo in contrast to the distinct responses shown by the Ottenby birds, are probably related to differences in migratory disposition between individuals at these two sites. Autumn robins captured at Falsterbo have low fat reserves and, according to ringing results as well as orientation experiments under overcast, are inclined to engage in reverse migration. As a consequence, they may show an increased tendency under clear skies to orient towards the sunset azimuth, perhaps an escape response directed to the brightest part of the sky, without consulting their magnetic compass sense (Sandberg et al. 1988).

Deflected Orientation

The mean orientation in most experimental categories falls close to south-southwest or north-northeast in relation to the shifted magnetic fields. Robins with a control orientation in northerly directions tend to shift their orientation towards geographical west-northwest, which corresponds to magnetic south-southwest or north-northeast depending on whether magnetic north has been shifted $+90^\circ$ or -90° . Only the spring experiments under simulated overcast with $mN -90^\circ$ deviate from this pattern. It is interesting to note that, although the majority of spring robins orient

towards geographical west-northwest in experiments with $mN +90^\circ$, a few prefer the opposite direction, suggesting axial rather than unimodal orientation.

For robins with a control orientation in southerly directions, as found during autumn at Ottenby, a bimodal pattern of directional choices along a north-northeast/south-southwest axis relative to the shifted magnetic fields is manifest. Hence, while spring robins in manipulated magnetic situations clearly prefer to orient towards the geographical west-northwest sector, the autumn birds at Ottenby show a greater inclination to choose also the opposite geographical east-southeast sector, and under simulated overcast there is even a predominance for the eastern end of the two sectors (Table I).

It seems plausible that the robins' orientation north-northeast/south-southwest in relation to the shifted magnetic fields reflects their normal axis of migration. These directions fit nicely with the mean direction of autumn (south-southwest) and spring (north-northeast) migration as revealed by ringing recoveries of passage migrants captured at Falsterbo and Ottenby (Sandberg et al. 1988).

Axial Orientation

Even if the robins correctly change their orientation along an axis north-northeast/south-southwest relative to the shifted magnetic fields, they apparently incorrectly estimate the polarity of the fields or, in cases with a balanced bimodality, they have difficulties in determining magnetic polarity. This indicates that the robins in our experiments do not use their magnetic compass as an inclination compass as suggested by Wiltschko & Wiltschko (1972) or by Kiepenheuer (1984). An inclination compass operating according to any one of these two hypotheses would have made it possible for the birds to determine the polarity of the shifted magnetic fields correctly.

Rather, one may suspect that there are additional cues by which the robins establish magnetic polarity. When the horizontal component of the magnetic field is aligned geographically west/east, the robins most often seem to interpret the westward end of this axis as north, particularly in spring and under simulated overcast in autumn. The fact that many autumn (and spring) robins orient in a westerly direction under clear skies may also be due

to an additional effect, unrelated to migratory orientation, of attraction towards the brighter parts of the twilight sky (Sandberg et al. 1988). The robins' orientation under opaque diffusing Plexiglas, simulating total overcast, makes it doubtful whether visual or celestial information are involved in the hypothetical cue(s) indicating magnetic polarity, although this possibility cannot be entirely ruled out.

In this context it is interesting that robins tested in orientation cages during late afternoon by Wiltschko & Höck (1972) often preferred directions in the northwest quadrant, both during spring and autumn and under clear and overcast skies. The orientation in this sector became even more distinct when magnetic north was shifted $+115^\circ$. Wiltschko & Höck (1972) interpreted these results as a bias caused by the cage construction (and how the birds were let into the cages), in combination with an intensified orientation when this biased preferred direction coincided with the typical axis of migration relative to the magnetic field. In our experiments we can exclude a similar cage-related bias (birds were let into the cages from below). In spite of this, there are obvious parallels between the orientation of our robins, particularly the Falsterbo birds, and the behaviour noted by Wiltschko & Höck (1972). Together these results indicate that migrants, when using the magnetic compass, as a first step perceive only the axial direction of the geomagnetic field. Perhaps they choose the seasonally appropriate end of this axis by some supplementary cue(s) that is involved in the mysterious attraction of migrants towards the geographical northwest quadrant (cf. also the so-called 'nonsense' orientation in this sector, Matthews 1961, 1984).

Axial rather than unidirectional orientation has been demonstrated for savannah sparrows tested indoors under diffusing panels of white plastic by Bingman (1981, 1983b). When he deflected the horizontal direction of the magnetic field under these conditions, the birds shifted their axis of orientation accordingly (Bingman 1981). In contrast, the orientation of savannah sparrows tested under clear sunset skies is unimodal in seasonally appropriate directions (Moore 1980). As mentioned above, Bingman (1983a) noted that, for young handraised savannah sparrows, the normal orientation under sunset skies was disrupted in a vertical magnetic field. These results may be interpreted as if migrants establish their orientation

axially in relation to the magnetic field, and that additional cues available during outdoor twilight tests allow the birds to discriminate between the two opposite alternatives. However, the lack of response to shifted magnetic fields, as reported by Moore (1985) for savannah sparrows in orientation experiments during twilight, run counter to this interpretation. Moore (1985) proposed that birds may learn celestial compass systems from their magnetic compass, so that with increasing age they are able to orient independently of magnetic stimuli to a greater degree.

Wiltschko & Wiltschko (1975) shifted magnetic north $+120^\circ$ in orientation experiments with robins under starry spring skies in Spain. In early tests, mainly at the end of March and beginning of April, the experimental robins showed a mean direction towards geographical north-northwest, which was significantly to the left of the mean north-northeast orientation of controls tested in the local geomagnetic field. In later tests, mainly at the end of April and beginning of May, the experimental birds changed their orientation towards geographical east-southeast, i.e. magnetic north. One may speculate that the robins in the early tests misjudged the polarity of the imposed magnetic field, and misoriented towards magnetic southwest instead of the intended northeast direction. Not until later in spring did they correctly determine the magnetic polarity, selecting appropriate northerly headings relative to the magnetic field. This would imply that cues used for assessing magnetic polarity show some seasonal change. However, the relatively small difference in mean orientation between early tests with $mN +120^\circ$ and control tests⁵ may be accidental (but compare the spring orientation of Falsterbo robins under $mN +90^\circ$, clear skies and Wiltschko & Höck 1972), as implicitly assumed by Wiltschko & Wiltschko (1975). If so, the results support the conclusion by these authors that the robins showed a delay in discovering the experimental shift in the magnetic field, because they rely extensively on their star compass for orientation, and only at long intervals do they use their magnetic compass to recalibrate the star compass.

Furthermore, Wiltschko & Wiltschko (1972) have demonstrated that robins tested indoors without access to visual directional cues orient in relation to the magnetic field and respond to reversals in magnetic polarity as if they use the angle of inclination to determine magnetic north.

Conclusions

We cannot exclude the possibility that unavoidable imperfections, although small, of the artificially generated magnetic field in the orientation cages (cf. above concerning the homogeneity of the magnetic field generated by the coils) may constitute a contributory cause of the unexpected deflections and bimodality in the orientation of the robins. Several studies have indicated that the orientation and/or navigation of birds may be affected by surprisingly small anomalies in the magnetic field (e.g. Keeton et al. 1974; Larkin & Sutherland 1977; Moore 1977; Walcott 1978; Kiepenheuer 1982; Alerstam 1987). However, it is difficult to draw any conclusions about the possible effect of such tiny deviations in the homogeneity of artificially generated magnetic fields as long as the process of magnetoreception in migrating birds remains unknown.

In summary, robins in our experiments most often changed their orientation when tested in artificially shifted magnetic fields during the twilight period after sunset, under clear skies as well as under overcast conditions. They generally adopted a north-northeast or south-southwest orientation relative to the shifted magnetic fields, which is in agreement with their typical axis of migration. Most remarkable was the change, demonstrated for Ottenby robins, from a unimodal southward autumn orientation in the normal geomagnetic field to axial orientation, with a rather balanced bimodality, when magnetic north was deflected $+90^\circ$ or -90° . In other cases, the robins changed their orientation as if they consistently misjudged the polarity of the shifted magnetic fields. These results probably cannot be explained solely with reference to the birds' magnetic compass sense. Rather, the results suggest that additional cues, available to the migrants in outdoor twilight tests under clear skies as well as overcast, are integrated with information from the geomagnetic field in the robins' orientation system. How this multi-cue system operates still defies our attempts of understanding.

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