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MAGNETIC ORIENTATION OF MIGRATORY WHEATEARS (*OENANTHE OENANTHE*) IN SWEDEN AND GREENLAND

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Summary

Orientation experiments were performed with wheatears (*Oenanthe oenanthe*) subjected to artificially manipulated magnetic fields, in Sweden and Western Greenland, during the autumn migration period. The objective was to compare responses by birds exposed to widely different geomagnetic conditions and, specifically, to clarify if birds are able to use magnetic cues for orientation at high geomagnetic latitudes, as in Western Greenland. Orientation experiments were run under clear sunset skies and under simulated total overcast. Clear-sky tests did not reveal any clearcut orientation responses by wheatears in deflected and vertical magnetic fields. There was a tendency, however, for previous experience of the relationship between geomagnetic cues and visual information to affect the birds' orientation in a vertical magnetic field. Under simulated overcast, the birds closely followed a 90° shift in magnetic direction in both study areas, and both samples failed to exhibit statistically significant mean directions when tested in vertical magnetic fields. The results clearly demonstrate that wheatears possess a magnetic compass. Furthermore, the birds are able to detect and use local geomagnetic information even at high magnetic latitudes in Western Greenland, notwithstanding the steep inclination (+81°) and large declination (−46°). A persistent attraction towards magnetic northwesterly headings, under both clear and overcast skies, is not consistent with migratory directions according to ringing recoveries and warrants further investigation.

Introduction

The idea that animals use geomagnetic information for orientation dates back more than a century (see review by Wiltschko and Wiltschko, 1988). Nonetheless, the magnetic compass of migratory birds was first described no more than about two decades ago. The directional behaviour of nocturnally migrating robins (*Erithacus rubecula*) in orientation cages was found to change in a predictable way when geomagnetic field directions were altered experimentally (Merkel and Wiltschko, 1965; Wiltschko, 1968). Since then, a growing number of species have

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been investigated, mainly nocturnal migrants, all of which seem to possess a magnetic compass (Wiltschko and Wiltschko, 1988).

The functional characteristics of the robin's magnetic compass were subjected to detailed analysis by Wiltschko and Wiltschko (1972), who reported the surprising discovery that these birds apparently do not use the polarity of the magnetic field to determine directions. Rather, the horizontal field component provides the birds with a pole–equator axis, the pole end of which is defined by the inclination of the magnetic field. This kind of compass mechanism has, more recently, also been demonstrated for garden warblers (*Sylvia borin*), pied flycatchers (*Ficedula hypoleuca*) and bobolinks (*Dolichonyx oryzivorus*) (Wiltschko, 1974; Beck and Wiltschko, 1982; Beason, 1989, but see Beason and Nichols, 1984). Recently, Sandberg *et al.* (1988*b*) tested robins in experimentally deflected magnetic fields and found that the birds displayed an axial response. The robins appeared unable to distinguish between poleward and equatorward directions on the basis of geomagnetic information alone, suggesting that additional cues are required to establish magnetic polarity.

Bird orientation during migration is also influenced by a variety of visual directional cues (Able, 1980; Wiltschko, 1983; Baker, 1984; Able and Cherry, 1985). For night-migrating species, two additional direction-finding systems may be important: the star compass (Sauer, 1957; Emlen, 1967*a*,*b*) and the position of the setting sun with its associated skylight polarization pattern (reviewed by Moore, 1987; Able, 1989). The complex interrelationships between visual and geomagnetic cues are not yet fully understood. Priorities between cues probably differ, not only among species, but also among individuals of different ages (Moore, 1984; Able and Bingman, 1987), body condition (Karlsson *et al.* 1988) or with dissimilar migratory experiences of geographical situations (Sandberg *et al.* 1988*a*,*b*).

It is an unresolved question how migratory birds orient at northerly geographic and geomagnetic latitudes, where they are faced with the following difficulties. (1) The sun compass: there are time compensatory problems during rapid longitudinal passages. (2) The star compass: stars are not visible during a large part of the arctic summer, i.e. they cannot be used at the time of spring arrival and they become visible only during late August, thereby restricting the possibilities for juvenile birds to aquire a functional star compass before the start of autumn migration; (3) The magnetic compass: a large inclination and declination make the geomagnetic field unreliable for orientation purposes within a wide region around the Magnetic North Pole (Alerstam, 1990; Alerstam *et al.* 1990).

To examine this problem, a two-year orientation cage study was designed to compare the relative importance of different directional cues, during twilight, for wheatears (*Oenanthe oenanthe*) from Sweden and Western Greenland. We were particularly interested to compare the birds' response to experimentally manipulated magnetic fields, at the two locations, which are at such different geomagnetic latitudes. Would Greenland wheatears be able to detect and use geomagnetic information in spite of the steep inclination (+81°) and large declination (−46°) in western Greenland, which is only about 1650 km from the Magnetic North Pole in Canada?

Orientation experiments were first conducted in Sweden, during autumn migration in 1988, to investigate if the orientation of Scandinavian wheatears could be influenced by experimental manipulations of the magnetic field. In 1989, the test equipment was shipped to the island of Disko on the west coast of Greenland, and a second experimental series was conducted here during the autumn, using exactly the same equipment with the identical setup and test procedure as used in Sweden.

Materials and methods

Experimental subjects and study areas

As test species we used the wheatear, a nocturnally migrating passerine, which breeds from the Atlantic coast of Europe to Alaska, with a distributional gap in high arctic Canada and reappearing in northeasternmost Canada, along the west coast of Greenland and in Iceland (Cramp, 1988). A vast majority of the wheatears from this immense breeding area migrates to winter grounds in Africa, south of the Sahara (Moreau, 1972). Ringing recoveries of Swedish wheatears reveal a general SW/SSW movement during autumn migration (Zink, 1973; Ottosson *et al.* 1990). Birds breeding in Greenland, in contrast, migrate initially towards the southeast until they reach the coasts of southwestern Europe, after which a shift to southwesterly headings presumably takes place (Salomonsen, 1967; Conder, 1989).

The first series of orientation experiments was conducted in southern Sweden from the second half of August until late September in 1988. Wheatears were either captured in mist nets while on migration (30 out of 41 individuals=73 %), at Falsterbo Bird Observatory (55° 23′N, 12° 50′E) and Ottenby Bird Observatory (56° 12′N, 16° 24′E), or collected during the summer as fledglings from nests (11 out of 41 individuals=27 %, Ottenby) and held in captivity until autumn migration commenced. Experiments were carried out in open meadows, simultaneously at Stensoffa Ecological Field Station (55° 42′N, 13° 25′E, Falsterbo birds) and at Ottenby about 3 km to the north of the observatory. The characteristics of the local geomagnetic field in South Sweden are shown in Fig. 1.

The second series of orientation tests was performed at the University of Copenhagen's Arctic Field Station in Godhavn (69° 18′N, 53° 40′W), situated on the island of Disko on the western coast of Greenland. These experiments started in late August and lasted until the middle of September in 1989. Nest sites of breeding wheatears were located during July and nestlings were removed from their nests, at an age of approximately 8–10 days, together with either the female or male. The young nestlings were subsequently raised indoors by one of their parents. Additional wheatears were captured in mist nets after the onset of migration, in the surroundings of the Arctic Field Station. The number of wheatears raised in captivity and subsequently used in the experiments constituted

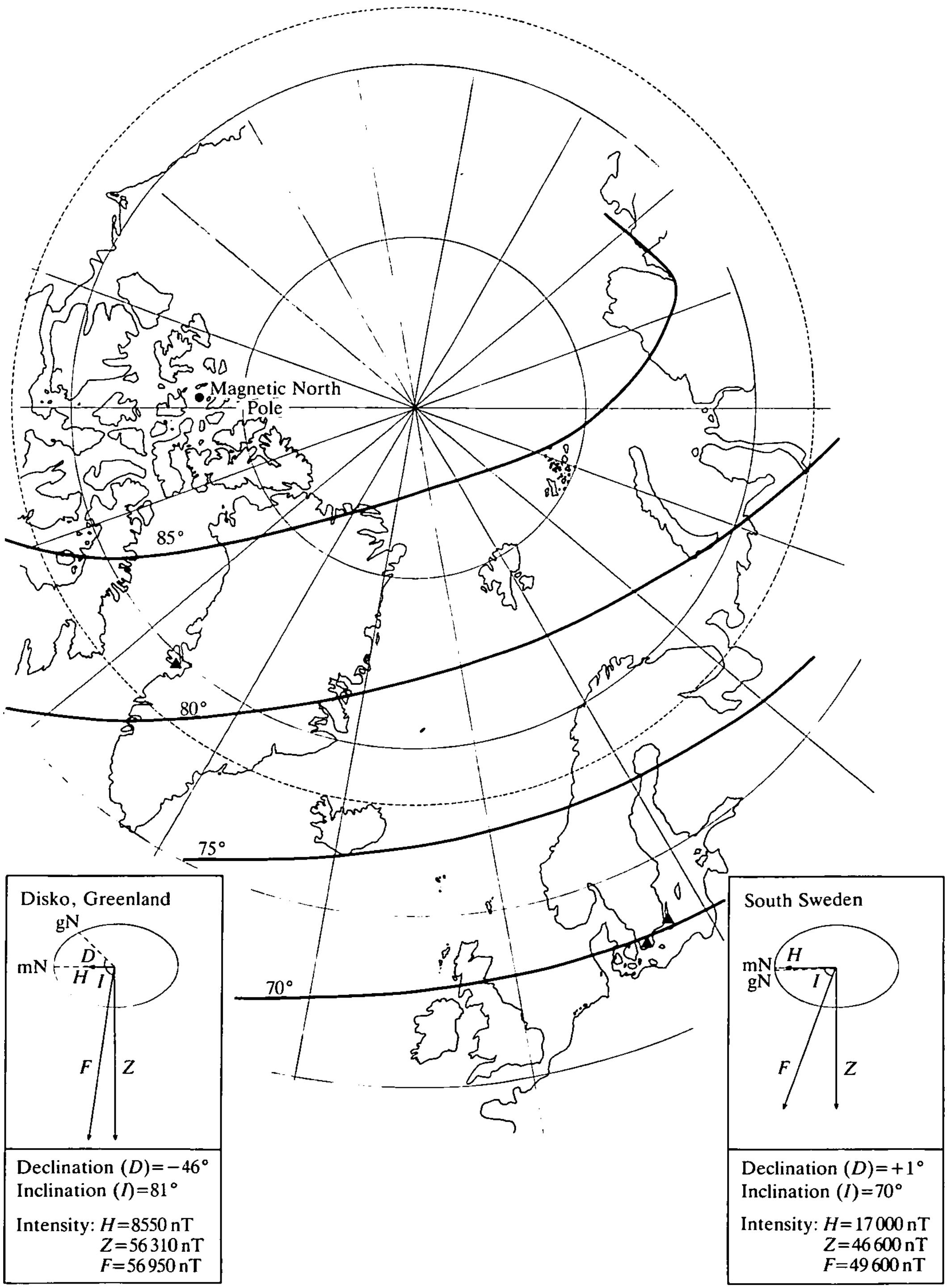
Magnetic North Pole
85°
80°
75°
70°
Disko, Greenland
gN
mN
D
H
I
F
Z
Declination (D)=−46°
Inclination (I)=81°
Intensity: H=8550 nT
Z=56 310 nT
F=56 950 nT
South Sweden
H
mN
gN
I
F
Z
Declination (D)=+1°
Inclination (I)=70°
Intensity: H=17 000 nT
Z=46 600 nT
F=49 600 nT

Fig. 1

Fig. 1. Location of the three study sites (filled triangles) in South Sweden and Greenland. Thick lines show the inclination of the geomagnetic field. Inset figures give the local characteristics of the Earth's magnetic field in South Sweden and Greenland. Geomagnetic information (epoch, 1985.0) for South Sweden is derived from charts issued by the Swedish Geological Survey, and for Disko from data obtained at Godhavn Geophysical Observatory during 1984 (published by the Danish Meteorological Institute, Department of Geophysics, Copenhagen, 1988).

55 % (28 out of 51 individuals) of the birds that were tested in orientation cages. Orientation tests were run outside the field station, in an open habitat of alpine heath. For details of the local geomagnetic field at Disko, see Fig. 1.

At the test sites, wheatears were held in individual cages from the time they were self-sufficient. Holding-cages were made of a wooden frame covered with plastic nets. The birds spent the time before and between orientation tests indoors, in rooms with windows facing south (Greenland), west (Stensoffa, Sweden) or north (Ottenby, Sweden), thereby maintaining the natural photoperiod. Hence, the hand-raised Greenland birds were able to see a limited portion of the sun's arc between approximately 09:00 h and 15:00 h through the windows, whereas the hand-raised Swedish birds did not have that opportunity. While held in captivity, the wheatears had access to unlimited amounts of mealworms, food-mix for insectivorous birds, dried ant pupae and fresh vitamin-enriched water.

Experimental equipment and test procedure

All orientation tests were performed in modified Emlen-funnels allowing automatic surveillance of migratory restlessness in eight 45° sectors. The orientation funnels were placed inside large plastic tubes (height 800 mm, diameter 600 mm), thus restricting the visible sky sector to 90° overhead (see Fig. 1 in Sandberg *et al.* 1988*a*). We manipulated the local geomagnetic field by using pairs of magnetic coils with a quadratic cross-section (800 mm × 800 mm). The coils were mounted on the outside surface of the screening tubes to hide them from the birds' view. By orienting such a pair of coils along a magnetic southwest/northeast axis (with horizontal field intensity generated by the coils $=\sqrt{2}$ times the local geomagnetic horizontal intensity), we were able to shift the position of magnetic north 90° counterclockwise with unaltered total field intensity and inclination. Within a radius of 100 mm from the centre of the orientation cage (the area where the test bird was, see Sandberg *et al.* 1988*a*) the calculated deviation from homogeneity of the artificial horizontal magnetic field was no more than 3 % along the coil axis and no more than 2 % perpendicular to this axis. We also compensated the horizontal component of the local geomagnetic field, thus creating a vertical field, by orienting the coils along a magnetic north/south axis (with horizontal field intensity generated by the coils made equal to the local geomagnetic horizontal intensity). The inclination of the resulting magnetic field was always within 2° of vertical according to inclinometer and magnetometer measurements. We used eight pairs of coils during both experimental series (see Sandberg *et al.* 1988*a*,*b*, for further details of test equipment).

The wheatears were tested for directional preferences under three different magnetic conditions, all of which were tested under both clear sunset skies (maximum three-eighths cloud cover) and simulated total overcast (a panel of 3 mm white diffusing Plexiglas was placed on top of the screening tube). The test order was close to random, with different birds tested simultaneously under all three conditions during each experimental occasion throughout the season.

The three different conditions were. (1) Control: the birds had access to the unmanipulated local geomagnetic field. (2) Deflected magnetic field: magnetic north was shifted 90° to the left, i.e. towards geographic west (Sweden) or southwest (Greenland). (3) Vertical magnetic field: wheatears were exposed to a magnetic field that did not contain any meaningful directional information (inclination close to 90°).

Handling of the birds as well as test equipment and procedure were identical in Sweden and Greenland. Test birds were placed in the orientation cages and carried to the test arena about 15 min before the time of local sunset. Measurements began 10 min after the sun had set, and the experiments lasted for 1 h.

Data analysis and statistics

Individual wheatears were tested only once under each experimental condition described above. Results from the orientation cages were subjected to vector calculation, yielding a mean heading for each individual and test. We excluded bird-hours that either showed too little activity (40 registrations minimum) or failed to manifest a reasonably well-defined orientation, where the criterion for exclusion was arbitrarily set to $Nr^2<3.0$ (N=number of counts, r=vector length, cf. Table 1). The value 3.0 was chosen such that if the criteria of the Rayleigh test had been met, it would correspond to $P=0.05$ (Batschelet, 1981). Because the within-test data points are not independent, it was not used as a measure of statistical significance, but simply as a yardstick for exclusion of bird-hours that yielded unreliable estimates of orientation. The mean headings obtained under each of the six test conditions were pooled to calculate sample mean vectors and axes of orientation using standard procedures described in Batschelet (1981).

Mean axes of orientation were chosen as the basis of analysis when the average vector length resulting from doubling the angles (r_2) was larger than the corresponding unimodal vector length (r). This procedure was used to obtain the best possible description of angular distributions. Orientation scatter was compared between samples by the 'test for the homogeneity of concentration parameters', and differences in mean angles between test categories were investigated by using the 'one-way classification test' (Mardia, 1972).

Results

The results of orientation experiments under clear skies are shown in Fig. 2, and

Table 1. *The number of bird-hours exluded because of either showing too little activity (IA=inactive) or failing to manifest a reasonably well-defined orientation (DO=disoriented,* $Nr^2<3.0$*, see Materials and methods) in relation to the total number of tests (TOT)*

Experimental condition		South Sweden IA/DO/TOT	Greenland IA/DO/TOT
Clear skies	Control	1/3/41	4/2/35
	Deflected	0/2/35	3/2/34
	Vertical	0/2/31	2/2/30
Simulated total overcast	Control	3/1/34	8/4/51
	Deflected	1/5/30	12/2/51
	Vertical	0/3/33	12/7/51

Chi-square tests did not reveal any significant differences between experimental categories either in Sweden or in Greenland. However, considering the total samples under clear skies and simulated total overcast, respectively, and comparing both within and between study sites, the following significant differences emerge according to chi-square tests: (1) Sweden, clear skies – Greenland, clear skies; number of inactive tests (1/9, $P<0.05$); (2) Sweden, overcast – Greenland, overcast; number of inactive tests (4/32, $P<0.001$); (3) Greenland, clear skies – Greenland, overcast; number of inactive tests (9/32, $P<0.01$). These results may indicate a stronger dependence on favourable weather conditions for Greenland wheatears.

the corresponding results of tests under simulated total overcast are illustrated in Fig. 3. As there were no discernible statistical differences between birds captured and tested at the two sites in Sweden (valid for all test conditions), either in choice of directions or in scatter of headings, these two groups have been pooled and are treated as one sample. Likewise, since we could not detect any differences in orientation behaviour between raised and captured wheatears, indicated by filled and open symbols respectively in Figs 2 and 3, these two categories were pooled for Swedish and Greenland tests.

Orientation under clear skies

Swedish wheatears, tested in the local geomagnetic field (see Fig. 1) selected a mean direction towards geographic and magnetic NW (Fig. 2). Greenland birds exhibited a mean orientation towards geographic W, corresponding to magnetic NW. These mean directions are not statistically different from the average sunset azimuths (95% confidence intervals: Sweden=±35°, Greenland=±39°). The angular difference from the mean sunset direction is virtually the same in both cases, but with opposite signs (+32° and −36°, respectively, Fig. 2).

When magnetic north was deflected 90° counterclockwise in relation to its normal position, the Swedish birds responded with a slight, nonsignificant shift (−38°) in mean direction to the left of controls. Although the expected angular change of −90° did not occur, the observed tendency of a counterclockwise shift may indicate a partial influence of the magnetic manipulation, i.e. a minority of the birds might have responded to the experimental shift whereas a majority did

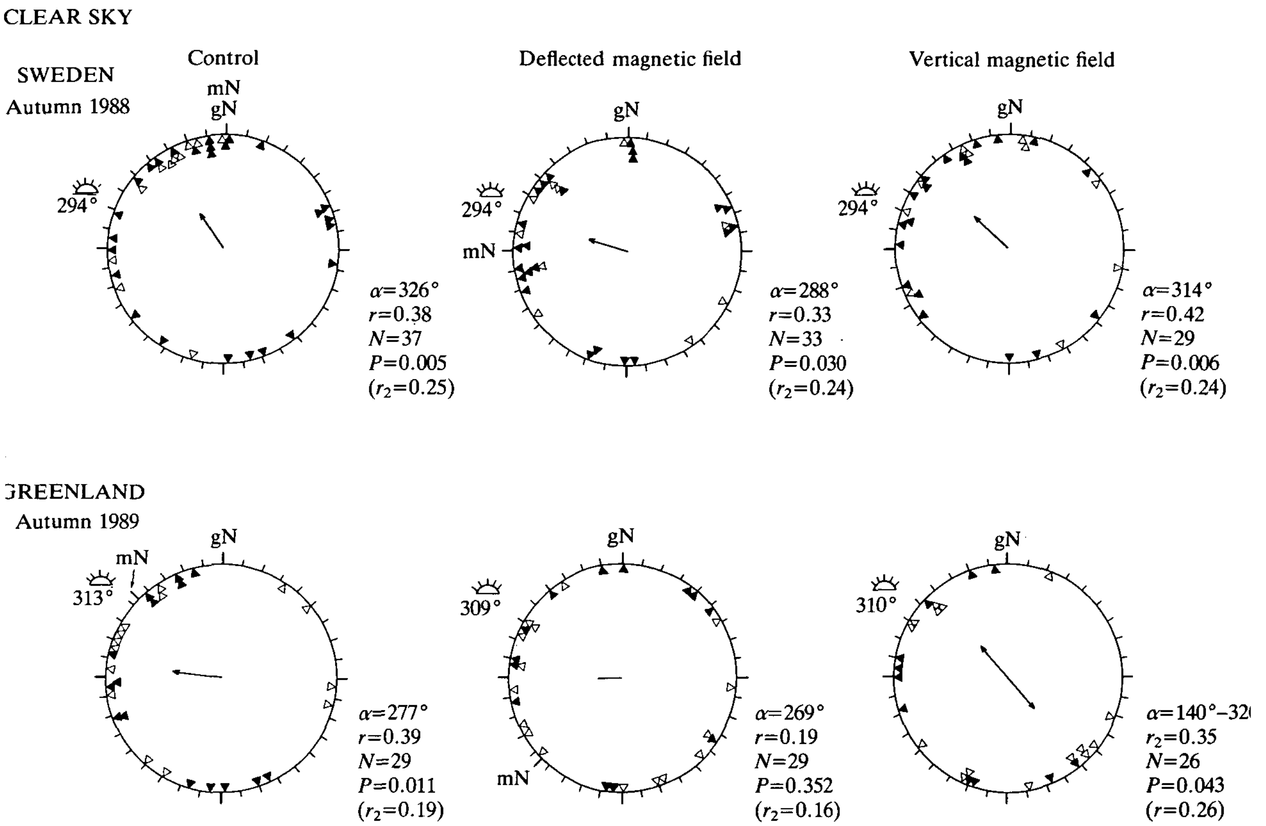

Fig. 2. Autumn orientation of wheatears under clear skies at sunset. Test results for Swedish wheatears are presented in the top row and the corresponding data for Greenland birds are shown in the bottom row. The left column shows the outcome of control experiments (unmanipulated local magnetic field), the middle column shows the orientation behaviour of the birds when magnetic north was experimentally deflected 90° counterclockwise, and in the right column results from tests in a vertical magnetic field are illustrated. The mean azimuth of the sun 40 min after sunset (i.e. in the middle of the test hour) is indicated outside each circular diagram. Likewise, the bearing of magnetic north (mN) is marked in relation to geographic north (gN). Each triangle represents the mean heading of one individual. Filled triangles illustrate headings of wheatears captured while on migration and open triangles denote birds that were raised indoors (see Materials and methods). The mean vector (α) of each sample is illustrated by an arrow or, in cases where a mean axis of orientation provided a better fit to the data, a double-ended arrow. Arrow lengths are proportional to the mean vector length (r or r_2) and are drawn relative to the radius of the circles (radius=1). Significance levels are according to the Rayleigh test (Batschelet, 1981).

not. Exposure to a deflected magnetic field (magnetic north=geographic southwest) resulted in a random distribution of headings for the Greenland birds. This could reflect a similar behavioural response to that shown by Swedish wheatears (see above), or it could be ascribed to a confusion effect caused by conflicting information from visual and geomagnetic cues.

When Swedish wheatears were tested in a vertical geomagnetic field, and thus deprived of meaningful magnetic directional information, they were still able to select a significant northwesterly course, almost identical to the mean direction under control conditions. Assuming that directional information can be transferred from geomagnetic to visual cues (see Wiltschko and Wiltschko, 1975*a*,*b*, 1976), we subdivided the sample into two categories depending on whether the preceding clear-sky experience was under a deflected (pD) or normal (pC) magnetic regime. The pD birds displayed an axial tendency (α=130°–310°, r_2=0.49, N=9, P<0.12) while the pC birds showed a more concentrated mean orientation towards NW (α=316°, r=0.59, N=20, P<0.001). In Greenland, orientation tests in a vertical magnetic field yielded a significant axial distribution of individual headings (Fig. 2, lower right diagram). Again, if we consider only those wheatears whose previous magnetic experience under clear skies was in a shifted geomagnetic field, these birds showed a mean directional tendency towards SE (α=153°, r=0.42, N=9, P<0.21). The remaining part of the sample (pC birds, see above) displayed a significant *unimodal* mean direction (α=269°, r=0.44, N=17, P<0.04), in good agreement with the average control direction. Hence, a transfer of geomagnetic information onto some visual cue(s) mediated by preceding magnetic experiences may be indicated for both Greenland and Swedish wheatears.

Orientation under simulated total overcast

When wheatears were tested in the local geomagnetic field without access to visual cues, both Swedish and Greenland birds displayed a very similar mean orientation compared with the outcome of control tests under clear skies (Fig. 3). There was a slight but insignificant increase in orientational scatter in both cases and the Swedish sample is on the limit of statistical significance. In spite of the fact that wheatears preferred seasonally incorrect migratory directions according to ringing recoveries (Ottosson *et al.* 1990), in Sweden as well as in Greenland, there was a remarkable consistency for selection of headings towards magnetic northwest, both with and without access to visual cues (compare Figs 2 and 3).

Furthermore, when the experimental birds were exposed to a shifted position of magnetic north, corresponding to geographic W (Sweden) or SW (Greenland), both groups responded with clear deflections of their mean orientation in the expected direction. The Swedish wheatears chose headings on average 71° to the left of controls. This is only 19° short of the expected amount of shift and significantly different from the result obtained in control tests (P<0.03). Greenland birds followed the experimentally induced change in magnetic directions even more closely and showed a significant counterclockwise deflection of 96° in relation to controls (P<0.01). Consequently, the observed orientation towards an approximate magnetic northwest direction is supported by the results obtained under shifted magnetic fields.

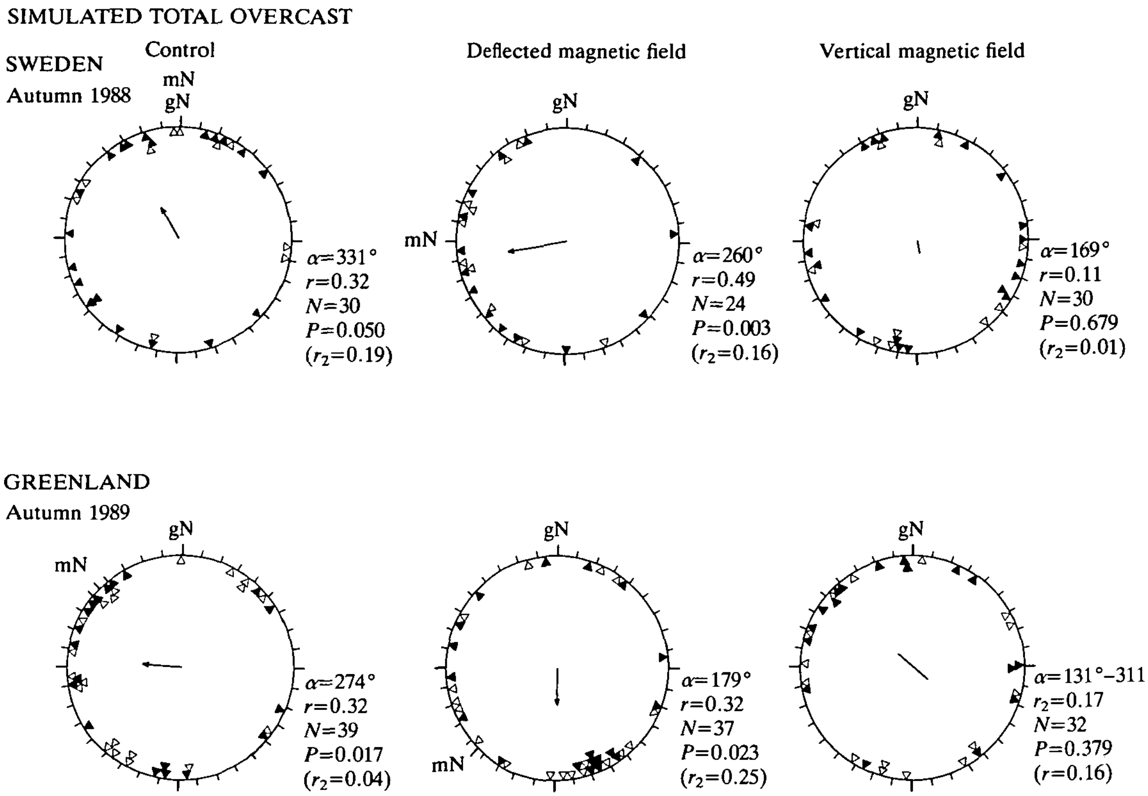

Fig. 3. Autumn orientation of wheatears under simulated total overcast during the twilight period in Sweden and Greenland. See Fig. 2 for further details.

In the absence of meaningful directional information from the geomagnetic field (vertical magnetic field) and from visual cues, the birds selected highly scattered headings both in Sweden and Greenland, resulting in randomly distributed samples according to the Rayleigh test.

Discussion

Magnetic orientation of wheatears

The experiments described here demonstrate that wheatears are able to detect and use the geomagnetic field as a directional reference, i.e. they possess a magnetic compass. Without access to visual cues (simulated total overcast, see Fig. 3), the birds tracked experimental shifts of the horizontal geomagnetic field direction closely, both in Sweden and Greenland. Furthermore, exposure to a vertical magnetic field resulted in random distributions. In contrast, under clear skies, both Swedish and Greenland wheatears were less influenced by experimental changes of the Earth's magnetic field (Fig. 2), thus pointing to the importance of visual cues available during the twilight period. There were indications that preceding experience of the relationship between geomagnetic and visual cues influenced the orientation behaviour of at least some individuals during subsequent clear-sky tests in a vertical magnetic field. For example, the bimodal distribution obtained under this condition in Greenland may be explained by the fact that birds whose immediately preceding clear-sky test was in a deflected field chose southeasterly headings, whereas the northwesterly headings mainly stemmed from individuals previously tested in the local geomagnetic field.

An analysis of ringing recoveries obtained during autumn migration revealed highly concentrated mean directions towards SSW/SW (α=210°, r=0.99, N=21, from Sweden) and about SE (α=128°, r=0.99, N=6, from Greenland) (Ottosson *et al.* 1990). In the light of these autumn migration directions, the mean orientation of wheatears in control tests, at both study sites, with almost identical results under clear and overcast skies, seems inexplicable. The orientation performance in Sweden and Greenland disclosed a persistent attraction towards a magnetic northwesterly mean direction. In contrast, when Swedish wheatears were tested without screening shields during autumn migration at Ottenby under clear sunset skies, thus being given a much more extensive view of the sky (about 160° as opposed to 90° in the present study), they chose directions in better agreement with ringing data (α=197°, r=0.56, N=23, P=0.001, Ottosson *et al.* 1990). Greenland birds, tested under the same visually unrestricted conditions, displayed a comparable tendency, even though a significant mean orientation failed to emerge (α=64°, r=0.27, N=14, P=0.36). Similarly, release experiments conducted with autumn-migrating wheatears, under clear starry skies in Sweden (α=236°, r=0.61, N=19, P<0.001) as well as in Greenland (α=144°, r=0.58, N=19, P=0.002) yielded mean directions in agreement with the angular distribution of ringing recoveries (Ottosson *et al.* 1990).

Taken together, these results indicate that geomagnetic information alone is not sufficient for a seasonally correct cage orientation by migratory naive wheatears, in either Sweden or Greenland. Instead, an unrestricted view of the sky, including the lower parts close to the horizon, seems to be of crucial importance.

Differential geomagnetic experiences have been shown to affect stellar orientation of a number of migrants (Wiltschko and Wiltschko, 1975*a*,*b*; 1976). Recently, Bingman and Wiltschko (1988) examined the relative importance of geomagnetic and solar cues for the orientation of dunnocks (*Prunella modularis*) at sunset. They tested two groups of birds, each of which experienced a different magnetic regime, and in subsequent experiments, in which the dunnocks were exposed to vertical magnetic fields, the two categories became axially oriented in significantly different directions. The authors concluded that the previous magnetic experience had a strong effect on the birds' sunset orientation if they did not have access to meaningful geomagnetic information. This conclusion is supported by the tendency displayed by wheatears examined in this study (see above).

Why magnetic northwest?

That migratory naive wheatears do not seem to be able to select a seasonally appropriate migratory direction solely on the basis of geomagnetic information may indicate that they use a combination of magnetic and other (probably visual) cues for orientation. The seemingly inexplicable magnetic northwesterly bearings may provide important clues about the functional characteristics of the magnetic compass of migratory birds. The first and most obvious possibility is that magnetic NW represents some sort of 'default behaviour', i.e. when the birds are placed in a situation that is too restricted for an accurate assessment of available orientation cues, they resort to a default response.

Another and perhaps more interesting possibility is that this peculiar behaviour has something to do with the birds' perception of the geomagnetic field. Assuming that the birds use a magnetic inclination compass for their orientation (Wiltschko and Wiltschko, 1972), they have to measure the inclination angle in relation to either the true vertical (gravity) or the horizontal. Since the wheatears examined in this study were prevented from seeing the lower parts of the sky including the horizon (under both clear and overcast skies), the birds may have been screened off from a crucial cue (the horizontal) required for a successful determination of the migratory direction.

Anyhow, the pronounced and enigmatic northwest orientation, that has been repeatedly observed among young passerines during their first autumn migration period (Wiltschko, 1980; Sandberg *et al.* 1988*a*), distinctly different from the seasonally appropriate migratory direction, clearly merits further attention.

The following major conclusions can be drawn from this orientation cage study. First, wheatears are able to orient in relation to the geomagnetic field, at high geographic and magnetic latitudes, notwithstanding the field's large inclination and declination. The results imply an acute degree of magnetic sensitivity in migratory birds and, if they use an inclination compass for direction finding, the potential range within which it can be used has to be extended. In other words, how close to the Magnetic North Pole is the magnetic compass still functional? Second, under simulated total overcast the birds appear to rely solely on geomagnetic cues for direction finding. Third, when tested under clear skies the wheatears are less influenced by experimental manipulations of the Earth's magnetic field, indicating a role for visual cues at sunset. There were some indications that preceding experience of the angular relationship between geomagnetic and visual cues influenced the orientation behaviour of individuals tested in the absence of geomagnetic directional cues (vertical magnetic field). Finally, the persistent attraction towards magnetic northwesterly directions, shown by both Swedish and Greenland wheatears, does not agree with the expected autumn migration routes for these populations and remains inexplicable.

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