The orientation behaviour of migrating birds is characterized by complex interrelated mechanisms and by flexibility in the use of different environmental sources of directional information, such as the sun, the skylight polarization patterns (particularly around sunset and sunrise), the rotation of the starry sky and the geomagnetic field (reviewed by Able, 1980, 1989; Able and Cherry, 1985; Baker, 1984; Moore, 1987; Wiltschko and Wiltschko, 1991). The first clearcut evidence that birds use the geomagnetic field for their migratory orientation was obtained by Merkel and Wiltschko (1965) and Wiltschko (1968), who carried out carefully controlled cage tests with nocturnally migrating robins (Erithacus rubecula) and found that the birds’ orientation could be experimentally manipulated by shifts of the magnetic north direction of the local geomagnetic field using Helmholz coils. Since that time, a growing number of bird species have been investigated, mainly nocturnal migrants, all of which seem to possess a magnetic compass (Wiltschko and Wiltschko, 1988; but see Åkesson, 1993, 1994, for possible exceptions).

The functional characteristics of the magnetic compass of migratory birds have been examined in a number of species: robins, garden warblers (Sylvia borin), pied flycatchers (Ficedula hypoleuca), blackcaps (Sylvia atricapilla), bobolinks (Dolichonyx oryzivorus), silvereyes (Zosterops lateralis) and yellow-faced honeyeaters (Lichenostomus chrysops), and all of these have been found to use an inclination compass (Wiltschko and Wiltschko, 1972; Wiltschko, 1974; Viehmann, 1979; Beck and Wiltschko, 1981; Beason, 1989; Wiltschko et al., 1993; Munro and Wiltschko, 1993). Experiments in which the vertical component of the magnetic field was reversed have clearly shown that these birds do not use the polarity of the magnetic field, but rather the axial course of the field lines and their inclination relative to gravity or the true horizontal. Hence, migratory birds distinguish between poleward and equatorward instead of between north and south.

Perhaps the most intriguing challenge to the orientation system of migratory birds is represented by species breeding at high geographic and geomagnetic latitudes. These migrants are faced with extreme properties of cue characteristics and availability. For example, the use of the sun compass involves problems of time compensation during rapid longitudinal passages, the stars are not visible during a large part of the arctic/antarctic summer, making the star compass useless at spring arrival and restricting the acquisition of a functional star compass for juvenile birds before their autumn migration starts, and finally, the steep inclination of the geomagnetic field may make the magnetic compass unreliable or even unusable (Alerstam, 1990; Alerstam et al., 1990; Sandberg et al. 1991).

Orientation tests were conducted with snow buntings (Plectrophenax nivalis) exposed to artificially manipulated magnetic fields, during both spring and autumn migration. Experiments were run under clear sunset skies and under simulated complete overcast. The birds closely followed experimental shifts of the magnetic fields during both seasons regardless of whether they had access to celestial cues. Clear-sky tests in vertical magnetic fields resulted in a significant bimodal orientation, the directionality of which was almost identical during spring and autumn. When the snow buntings were deprived of celestial directional information and tested in vertical magnetic fields, they failed to show any statistically significant mean directions in either spring or autumn. The results demonstrate that snow buntings possess a magnetic compass and suggest that magnetic cues are of primary importance for their migratory orientation while on passage through temperate-zone areas. However, the axial orientation in vertical magnetic fields under clear skies may indicate an involvement of celestial cues as an auxiliary source of directional information.

Key words: birds, migration, orientation, geomagnetic field, Plectrophenax nivalis, snow bunting.

**Introduction**

The orientation behaviour of migrating birds is characterized by complex interrelated mechanisms and by flexibility in the use of different environmental sources of directional information, such as the sun, the skylight polarization patterns (particularly around sunset and sunrise), the rotation of the starry sky and the geomagnetic field (reviewed by Able, 1980, 1989; Able and Cherry, 1985; Baker, 1984; Moore, 1987; Wiltschko and Wiltschko, 1991). The first clearcut evidence that birds use the geomagnetic field for their migratory orientation was obtained by Merkel and Wiltschko (1965) and Wiltschko (1968), who carried out carefully controlled cage tests with nocturnally migrating robins (Erithacus rubecula) and found that the birds’ orientation could be experimentally manipulated by shifts of the magnetic north direction of the local geomagnetic field using Helmholz coils. Since that time, a growing number of bird species have been investigated, mainly nocturnal migrants, all of which seem to possess a magnetic compass (Wiltschko and Wiltschko, 1988; but see Åkesson, 1993, 1994, for possible exceptions).

The functional characteristics of the magnetic compass of migratory birds have been examined in a number of species: robins, garden warblers (Sylvia borin), pied flycatchers (Ficedula hypoleuca), blackcaps (Sylvia atricapilla), bobolinks (Dolichonyx oryzivorus), silvereyes (Zosterops lateralis) and yellow-faced honeyeaters (Lichenostomus chrysops), and all of these have been found to use an inclination compass (Wiltschko and Wiltschko, 1972; Wiltschko, 1974; Viehmann, 1979; Beck and Wiltschko, 1981; Beason, 1989; Wiltschko et al., 1993; Munro and Wiltschko, 1993). Experiments in which the vertical component of the magnetic field was reversed have clearly shown that these birds do not use the polarity of the magnetic field, but rather the axial course of the field lines and their inclination relative to gravity or the true horizontal. Hence, migratory birds distinguish between poleward and equatorward instead of between north and south.

Perhaps the most intriguing challenge to the orientation system of migratory birds is represented by species breeding at high geographic and geomagnetic latitudes. These migrants are faced with extreme properties of cue characteristics and availability. For example, the use of the sun compass involves problems of time compensation during rapid longitudinal passages, the stars are not visible during a large part of the arctic/antarctic summer, making the star compass useless at spring arrival and restricting the acquisition of a functional star compass for juvenile birds before their autumn migration starts, and finally, the steep inclination of the geomagnetic field may make the magnetic compass unreliable or even unusable (Alerstam, 1990; Alerstam et al., 1990; Sandberg et al. 1991).
In order to shed light on this problem, we chose to examine the orientation performance and cue integration of snow buntings (Plectrophenax nivalis) on passage migration through temperate-zone areas. We compared the relative importance of different directional cues for the migratory orientation of a species that breeds in the high Arctic in order to investigate whether snow buntings show any differences in cue use relative to temperate-zone birds. Orientation tests were conducted in southeast Sweden during both spring and autumn migration.

**Materials and methods**

**Study species and general information**

The snow bunting, a mainly nocturnal migrant in temperate-zone areas, is circumpolarly distributed, breeding on the Arctic tundra and locally in the adjoining boreal climatic zones (Voous, 1960; Bezzel, 1993). It is, in fact, the most northerly recorded passerine, with one known sighting at the North Pole (Godfrey, 1986). The wintering grounds of this species are circumboreal within the northern temperate zone (Voous, 1960; Nethersole-Thompson, 1966). However, data on population-specific wintering areas are scant, mainly because of a basic lack of ringing recoveries.

The present series of orientation cage experiments was conducted in southeast Sweden at Ottenby Bird Observatory (56°12′ N, 16°24′ E). Tests were performed during three migration seasons: 13 March – 3 April 1990, 21 February – 15 March 1991, and 20 November – 18 December 1991. Snow buntings were captured while on passage migration by using mist-nets and walk-in traps. All experiments were carried out at the same test arena, situated in an open meadow located approximately 3 km north of the observatory. At this site, the birds were held indoors in spacious individual cages constructed from a wooden frame covered with fine-meshed plastic net. The buntings spent the time before and between different orientation tests in a room with windows to maintain the natural photoperiod, and they were exposed to the local geomagnetic field. While held in captivity, for a maximum of 2 weeks, the birds had access to food *ad libitum*, consisting of summer rape seeds (*Brassica napus*) supplemented with live mealworms (*Tenebrio sp.*) and fresh vitaminized water.

**Equipment and test protocol**

Orientation experiments were performed using modified Emlen funnels with automatic registration of the migratory activity in eight tangential 45° sectors (see Sandberg et al. 1988a, for a detailed description of the orientation cages). The funnels were placed on top of plastic crates, positioning the cage at 0.5 m above ground level. No screening devices were used and the birds could see approximately 160° of the sky overhead, including most of the lower portion of the twilight sky (see Sandberg, 1991). We manipulated the local geomagnetic field by using pairs of magnetic coils with a quadratic cross section (800 mm × 800 mm, see Sandberg et al. 1988b, for a detailed description and information on the homogeneity of the artificial magnetic field). Depending on the orientation of the coils, we could either shift the position of magnetic north maximally ±120° from normal or compensate the horizontal component of the geomagnetic field to create a vertical field (inclination = 90°). The inclination of the resulting vertical magnetic field deviated by less than 2° from the true vertical according to inclinometer and magnetometer measurements. We used eight pairs of coils, which were placed around the orientation cages. This arrangement was identical for all the birds tested irrespective of whether the coils were activated.

The local characteristics of the geomagnetic field were as follows: horizontal intensity 17 μT, vertical intensity 46.6 μT, total intensity 49.6 μT, with an angle of inclination at 70° and declination at +1°. These magnetic parameters remained unaltered in the artificially shifted magnetic fields, except in vertical fields where the total intensity equaled the vertical intensity, with horizontal intensity approximately 0 μT (see also below). The reduction in total intensity (~6%) in vertical fields was within the functional range shown for other migratory bird species (see Wiltshcko and Wiltshcko, 1988).

The snow buntings were tested for their directional preferences under both clear sunset skies (maximum four-eights cloud cover with the setting sun always visible) and simulated complete overcast. To simulate overcast, a panel of 3 mm opaque diffusing Plexiglas was placed on top of the orientation cage, preventing the test birds from seeing the sky and making it unlikely that the buntings were able to perceive any celestial cues under this condition. Laboratory measurements showed that the degree of polarization of 100% polarized light was reduced to between 7% (blue light, 488 nm) and 13% (red light, 633 nm) after passing through such a panel. Under both these conditions (with or without access to celestial cues), the birds were exposed to three different magnetic field regimes. The test sequence was randomized as far as possible, and different individuals were tested simultaneously under all three magnetic conditions at each experimental occasion throughout the season.

The three different magnetic regimes were as follows: (1) control, the birds had access to the unmanipulated local geomagnetic field; (2) deflected magnetic field, magnetic north was shifted 90° counterclockwise, i.e. towards geographic west (spring experiments), or 90° clockwise towards geographic east (autumn tests); (3) vertical magnetic field, snow buntings were exposed to a magnetic field that did not contain any meaningful directional information (inclination close to 90°).

The buntings were put into the orientation cages indoors about 20 min before local sunset and were then immediately carried to the test arena. This procedure allowed the birds to calm down and also gave them the opportunity to calibrate the available directional information before registration began approximately 10 min after the sun had set. All experiments lasted for 1 h.

**Data analysis and statistical evaluation**

Individual snow buntings were tested only once under each
different experimental condition described above (spring, 217 test hours/55 individuals; autumn, 72 test hours/20 individuals; i.e. each individual participated on average in 3–4 different tests). Activity distributions obtained from the orientation cages were subjected to vector calculation, resulting in a mean heading for each individual and test (Batschelet, 1981). We excluded bird-hours that either showed too little activity (minimum set at 40 registrations), or failed to show a reasonably well-defined orientation, where the criterion was arbitrarily set to $N \leq 3.0$ (where $N$ is the number of counts and $r$ is the vector length; see 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, the Rayleigh test was not used as a measure of statistical significance, but simply as an indicator for exclusion of bird-hours that yielded unreliable estimates of orientation. The total number of excluded bird hours according to these criteria was 21 during spring and three during autumn (see Table 1). Mean headings obtained under each of the six experimental 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 mean unimodal vector length ($r$). Scatter of headings around the mean angle was compared between samples by using the ‘test for the homogeneity of concentration parameters’ (indicated by $r$; Mardia, 1972), and differences in mean angles between test categories were investigated by using the ‘one-way classification test’ (indicated by $F_1,df$; Mardia, 1972). The latter test allows two-sample comparisons independent of mean vector lengths as long as the vector lengths are not significantly different between the samples under investigation. If one or both of the involved samples were randomly distributed, or if the vector lengths were significantly different from each other, the Watson’s $U^2$-test (indicated by $U^2$) was applied (Batschelet, 1981).

**Results**

The directional behaviour of snow buntings during spring and autumn migration is illustrated in Figs 1 and 2, respectively. Since the orientation of the birds during the two spring migration seasons did not differ significantly in any aspect (mean directions, scatter of headings), the spring data have been pooled and will be treated as one sample.

**Orientation during spring migration**

Snow buntings tested in the local geomagnetic field under clear skies chose a mean direction towards NNW (Fig. 1). When magnetic north was deflected $90^\circ$ counterclockwise from its normal position, the birds responded with a significant counterclockwise shift in mean direction of $92^\circ$ ($F_{1,69}=17.1, P<0.001$). In the absence of meaningful directional information from the geomagnetic field (vertical field) but with access to celestial cues, the birds oriented along a significant NNW–SSE mean axis. This axis is situated $31^\circ$ counterclockwise from the band of maximum polarization at the time of the test (compare sunset direction, Fig. 1).

To investigate whether this bimodal orientation under clear skies in a vertical magnetic field resulted from a transfer of directional information from the magnetic field onto celestial cues during preceding tests, as has previously been shown for dunnocks (*Prunella modularis*) and wheatears (*Oenanthe oenanthe*) (Bingman and Wiltschko, 1988; Sandberg et al., 1991; see also Wiltschko and Wiltschko, 1975a,b, 1976), we subdivided the sample into two categories depending on whether the preceding clear-sky exposure was under a deflected (pD) or normal (pC) magnetic regime. The pD birds showed a significant axial mean orientation ($\alpha_z=164–344^\circ$, $r_z=0.42$, $N=20$, $P<0.05$) and the pC birds showed an axial tendency with similar directionality ($\alpha_z=159–339^\circ$, $r_z=0.42$, $N=7$, $P>0.05$). Hence, a transfer of geomagnetic information onto some visual cue(s) was not evident.

When snow buntings were tested in an unmanipulated geomagnetic field without access to celestial cues (simulated complete overcast), they selected a well-defined northerly mean direction which was not significantly different from the mean direction chosen by clear-sky controls ($F_{1,71}=3.9, P>0.05$). The birds shifted their mean direction $85^\circ$ counterclockwise when exposed to an experimentally deflected magnetic field under complete overcast. This shifted mean direction was significantly different from the control direction ($F_{1,85}=21.2, P<0.001$). Without access to meaningful directional information from either celestial or magnetic cues (vertical magnetic field, simulated overcast), the buntings selected highly scattered headings, resulting in a sample not significantly different from random.

**Table 1. Number of tests excluded based on either inactivity (IA, <40 counter registrations per hour) or showing disorientation (DO, $N^2 < 3.0$, cf. Materials and methods) relative to the total number of birds tested (TOT)**

<table>
<thead>
<tr>
<th>Experimental condition</th>
<th>Spring tests</th>
<th>Autumn tests</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>IA</td>
<td>DO</td>
</tr>
<tr>
<td>Clear skies</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Deflected</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Vertical</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Complete overcast</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>Deflected</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Vertical</td>
<td>3</td>
<td>0</td>
</tr>
</tbody>
</table>

Chi-square tests did not reveal any statistically significant differences between experimental categories during either spring or autumn migration. The only significant difference was between the total number of inactive tests under clear skies and those under complete overcast conditions during spring (number of inactive tests: 4 versus 14, $P<0.05$).

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Orientation during autumn migration

Under clear autumn skies, snow buntings selected a mean direction towards SW (Fig. 2). Although sample sizes were small for the two experimental categories, the buntings followed the clockwise shift of the geomagnetic field closely (93° clockwise from the controls; $F_{1,25}=9.5$, $P<0.01$) and displayed a mean axis of orientation in the vertical field which was almost identical to the result obtained during spring migration (compare Fig. 1). In relation to the band of maximum polarization, however, this mean axis of orientation differed by 19° counterclockwise (compare spring data).

Orientation tests under complete overcast revealed a mean control direction towards SW, very similar to the corresponding result under clear skies. Again, in the deflected magnetic field, the birds followed the experimental shift and their mean direction was 8° clockwise from the control direction ($U^2=0.4$, $P<0.001$). The headings of the deflected birds were also significantly more concentrated than those of the controls ($t=-2.0$, $P<0.05$). Without directional information from either celestial or geomagnetic cues (vertical magnetic field, simulated overcast), the buntings failed to show a significant mean direction.

Discussion

Magnetic orientation of snow buntings

The experiments presented here clearly demonstrate that snow buntings are capable of detecting and using the geomagnetic field for their orientation. In fact, the similarity of the results obtained with and without access to celestial cues, during both spring and autumn migration, seems to suggest that snow buntings rely primarily on their magnetic compass for migratory orientation around sunset.

In this respect, our results are similar to the findings reported by Bingman and Wiltschko (1988) in outdoor experiments with spring-migrating dunnocks. Those authors tested dunnocks under clear skies at sunset and found that the Earth’s magnetic field was the primary directional reference, i.e. the birds closely followed an experimental clockwise shift of magnetic north. Furthermore, the dunnocks displayed an axial response in a
Magnetic orientation of snow buntings

Vertical magnetic field which was shown to depend on previous experience of the relationship between geomagnetic and celestial cues. Thus, dunnocks seemed to transfer directional information from the geomagnetic field onto some visual cue(s). A similar information transfer was indicated in orientation experiments with wheatears (see Sandberg et al. 1991). Although our snow buntings also became axially oriented when they had access to celestial cues only (vertical magnetic field), there were no indications of an information transfer from magnetic to visual cues in our data set. This may indicate a more independent use of celestial cues in the orientation system of snow buntings compared with dunnocks.

The bimodal orientation shown by snow buntings tested under clear skies in a vertical magnetic field, during both spring and autumn migration, may provide a hint towards identification of the relevant celestial cue that was involved. It is difficult to imagine that asymmetrical cues, such as the horizon glow from the setting sun or local landmarks such as nearby trees, could be manifested as an axial directional response. However, the E-vector of polarized skylight is a prominent directional source at the time of sunset (Brines and Gould, 1982), which is apparently used as an axial reference for orientation (Able, 1982, 1989). The bimodal orientation of snow buntings in vertical magnetic fields may thus reflect the use of the E-vector of polarized skylight as an auxiliary source of directional information. The fact that the birds’ mean orientation relative to the E-vector differed between spring and autumn tests could be interpreted as follows: when information from the primary cue (magnetic field) is lacking, the birds are able to use back-up information (polarized light) to find, at least approximately, their preferred migratory direction. However, the lack of a firm database regarding the expected migratory direction (no ringing recoveries available from the test site) during both autumn and spring makes it difficult to analyze the orientation performance of snow buntings in relation to skylight polarization cues, and any interpretation must therefore remain speculative.

A comparison of the control directions obtained during spring and autumn reveals that preferred headings were not exactly opposed between seasons. Unfortunately, because of the scarcity of ringing recoveries, we do not know the location of either the breeding grounds or the wintering area of our test birds. So far, there are only two recoveries of snow buntings ringed in Sweden: one individual ringed (18 March 1984) at Nidingen (57°18′ N, 11°54′ E), an island just off the Swedish west coast, which was found dead (14 May 1984) on an oil platform in the North Sea (60°57′ N, 0°56′ E), and one bird ringed (20 April 1983) at Abisko (68°21′ N, 18°49′ E) in northern Sweden, which was found dead 7 days later at Tromsø (69°36′ N, 18°50′ E) in Norway. These two spring recoveries seem to suggest potential breeding areas between Iceland in the west and the northern part of the Scandinavian Peninsula in the east. Our orientation data seem to indicate northern Scandinavia as the most likely breeding area and northwestern

Fig. 2. Autumn orientation of snow buntings (Plectrophenax nivalis) under both clear skies and simulated complete overcast during the twilight period. See legend to Fig. 1 for further details.
continental Europe as a potential wintering area. If the snow buntings tested belonged to the same population, then a change in migratory direction (‘Zugknicke’) within seasons would be implied. Alternatively, since the deviation from a 180° reversal between spring and autumn directions was most pronounced in the clear-sky tests, one may speculate that the buntings showed a compromise orientation between a partial attraction towards the setting sun and their intended ‘pure’ magnetic heading (compare overcast control tests), especially in spring (see also Åkesson and Sandberg, 1994).

In contrast to the present study, and that of Bingman and Wiltschko (1988), the majority of other studies examining migratory orientation at twilight have emphasized the primary importance of visual cues (reviewed by Moore, 1987; Able, 1989; see also Katz, 1985). The underlying reason(s) for these differences remains unclear, but could be attributed to interspecific differences in orientation cue integration or may reflect the migratory situation, especially in relation to ecological barriers, in which the migrants find themselves (see Sandberg et al. 1988a; Sandberg, 1991).

Previous findings suggest that magnetic orientation in birds is based on a common mechanism, namely the inclination compass (Wiltschko et al. 1993; but see Beason and Nichols, 1984). However, other vertebrates, such as the sockeye salmon (Oncorhynchus nerca) and the African mole rat (Cryptomys hottentotus), and invertebrates, such as the flour beetle (Tenebrio molitor) and the western Atlantic spiny lobster (Panulirus argus), have been shown to possess magnetic compasses based on the polarity of the field rather than the inclination (Quinn et al. 1981; Marhold et al. 1991; Arendse, 1978; Lohmann et al. 1995). Interestingly, the red-spotted newt (Notophthalmus viridescens) appears to possess two different types of magnetic compass, an inclination compass for simple-compass orientation towards the shoreline of the home pond and a polarity compass for use in true navigation after displacements from home (Phillips, 1986).

Given the existence of two different magnetic orientation mechanisms, even within species, it might be reasonable to ask whether this is a common feature for all vertebrates/organisms. If so, it would be especially interesting to examine the functional characteristics of magnetic orientation in species, such as snow buntings, which are faced with extreme properties of cue characteristics, i.e. species living at or migrating through high (polar) or low (equatorial) geomagnetic latitudes (see Wiltschko and Wiltschko, 1992). Access to both inclination and polarity compasses may provide a flexible geomagnetic orientation system rendering functionality even in the most extreme cue situations. One could well imagine ‘grey zones’ within which one or the other of the two different systems would remain usable.

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