

ORIENTATION OF SNOW BUNTINGS (*PLECTROPHENAX NIVALIS*) CLOSE TO THE MAGNETIC NORTH POLE

ROLAND SANDBERG*, JOHAN BÄCKMAN AND ULF OTTOSSON

Department of Animal Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden

*e-mail: Roland.Sandberg@zooekol.lu.se

Accepted 19 March; published on WWW 21 May 1998

Summary

Orientation experiments were performed with first-year snow buntings (*Plectrophenax nivalis*) during their autumn migration in a natural near-vertical geomagnetic field approximately 400 km away from the magnetic north pole. Migratory orientation of snow buntings was recorded using two different techniques: orientation cage tests and free-flight release experiments. Experiments were performed under clear skies, as well as under natural and simulated complete overcast. Several experimental manipulations were performed including an artificial shift of the E-vector direction of polarized light, depolarization of incoming light and a 4 h slow clock-shift experiment. The amount of stored fat proved to be decisive for the directional selections of the buntings. Fat individuals generally chose southerly mean directions, whereas lean birds selected northerly headings. These directional selections seemed to be independent of experimental manipulations of the buntings' access to visual cues even in the local near-

vertical magnetic field. Under clear skies, the buntings failed to respond to either a deflection of the E-vector direction of polarized light or an experimental depolarization of incoming skylight. When tested under natural as well as simulated overcast, the buntings were still able to select a meaningful mean direction according to their fat status. Similarly, the free-flight release test under complete overcast resulted in a well-defined southsoutheast direction, possibly influenced by the prevailing light northwest wind. Clock-shift experiments did not yield a conclusive result, but the failure of these birds to take off during the subsequent free-flight release test may indicate some unspecified confusion effect of the treatment.

Key words: bird, migration, orientation, magnetic north pole, *Plectrophenax nivalis*, snow bunting.

Introduction

The ability of migratory birds to find the correct flight routes while travelling between breeding and wintering areas has inspired human thought for centuries (e.g. Alerstam, 1990a) and has led to numerous ingenious investigations concerning orientation performance (for a review, see Berthold, 1991). It has been convincingly demonstrated that migratory birds can derive compass information from several different environmental sources, including both celestial and geomagnetic cues (for reviews, see Moore, 1987; Wiltschko and Wiltschko, 1991). Exactly which of the available cues is primarily used in a specific situation may vary according to the age and experience of the test birds (Moore, 1984; Able and Bingman, 1987), the ecological context within which experiments are performed (Sandberg *et al.* 1988a,b; Sandberg, 1991; Pettersson *et al.* 1991; Sandberg and Moore, 1996) and the energetic status of test subjects (Karlsson *et al.* 1988; Sandberg, 1994; Sandberg and Moore, 1996; Bäckman *et al.* 1997). The diversity of factors that influence orientation decisions has led to a consensus in the scientific community about the flexible character of avian migratory orientation systems (e.g. Able and Able, 1996).

Since the discovery that nocturnally migrating robins (*Erithacus rubecula*) are able to use geomagnetic cues for their orientation (Wiltschko, 1968), a growing number of bird species has been investigated, mainly nocturnal migrants, all of which seem to possess a magnetic compass (Wiltschko and Wiltschko, 1995). For some of these species, the functional characteristics of the magnetic compass have been examined (Wiltschko and Wiltschko, 1972; Wiltschko, 1974; Viehmann, 1979; Beck and Wiltschko, 1981; Beason, 1989; Wiltschko *et al.* 1993; Munro and Wiltschko, 1993; Bletz *et al.* 1996). The usual techniques employed in these studies include artificial reversals of the vertical component of Earth-strength magnetic fields. The fact that the test birds follow the reversal clearly show that they do not use the polarity of the magnetic field, but rather the axial course of the field lines and their inclination.

Recently, Sandberg and Pettersson (1996) showed that snow buntings (*Plectrophenax nivalis*) have access to a magnetic compass and that they use it as a primary tool for orientation while on passage migration through temperate-zone areas. Snow buntings breed in the high Arctic and were deliberately

chosen as test subjects in the former study to pave the way for a second series of comparative experiments close to the magnetic north pole (NMP). The area around the NMP is especially interesting because (1) the magnetic field lines enter the Earth at sufficiently steep angles ($>88^\circ$ within 500 km of the pole) to render an inclination compass useless (evidence from experimentally simulated vertical fields; see Wiltschko and Wiltschko, 1995), and (2) stars are not visible until mid-August, making it difficult for young birds to acquire a functional star compass before the autumn migration commences (Alerstam, 1990b; Alerstam *et al.* 1990). According to present knowledge, the only remaining option available for the development of a functional compass should be based on the celestial rotation of solar cues (the sun itself and the associated skylight polarization patterns; Able and Able, 1996). The current study was performed at Resolute, Cornwallis Island, Canada, during the autumn migration period, using snow buntings as test subjects.

Materials and methods

Test birds and study area

Snow buntings (*Plectrophenax nivalis*) usually migrate in

small, loose flocks (e.g. Salomonsen, 1950). Close to the wintering areas, both nocturnal and diurnal migration have been observed (Roberts, 1932), but in Arctic regions these birds primarily show nocturnal migratory behaviour (Salomonsen, 1950; Parmelee, 1968). The buntings breed circumpolarly on the Arctic tundra (Voous, 1960; Nethersole-Thompson, 1966), but information about population-specific wintering destinations is scant. In Canada, autumn departure of snow buntings from high arctic islands (latitude $75\text{--}80^\circ\text{N}$) starts around mid-August and may continue well into September (Lyon and Montgomerie, 1995).

The series of orientation experiments presented in this paper was run at the Polar Continental Shelf Projects research station in Resolute ($74^\circ41'\text{N}$, $94^\circ54'\text{W}$), situated on Cornwallis Island in arctic Canada (Fig. 1), during August 1992. Snow buntings were captured in the vicinity of the research station from the beginning of August. Experiments were carried out from 11 to 30 August in an open area adjacent to the station. The birds were held indoors in individual cages constructed out of non-magnetic materials, in a room with windows to maintain the natural photoperiod. While held in captivity, the buntings had access to unlimited amounts of food consisting of mixed bird seeds and fresh vitaminized water.

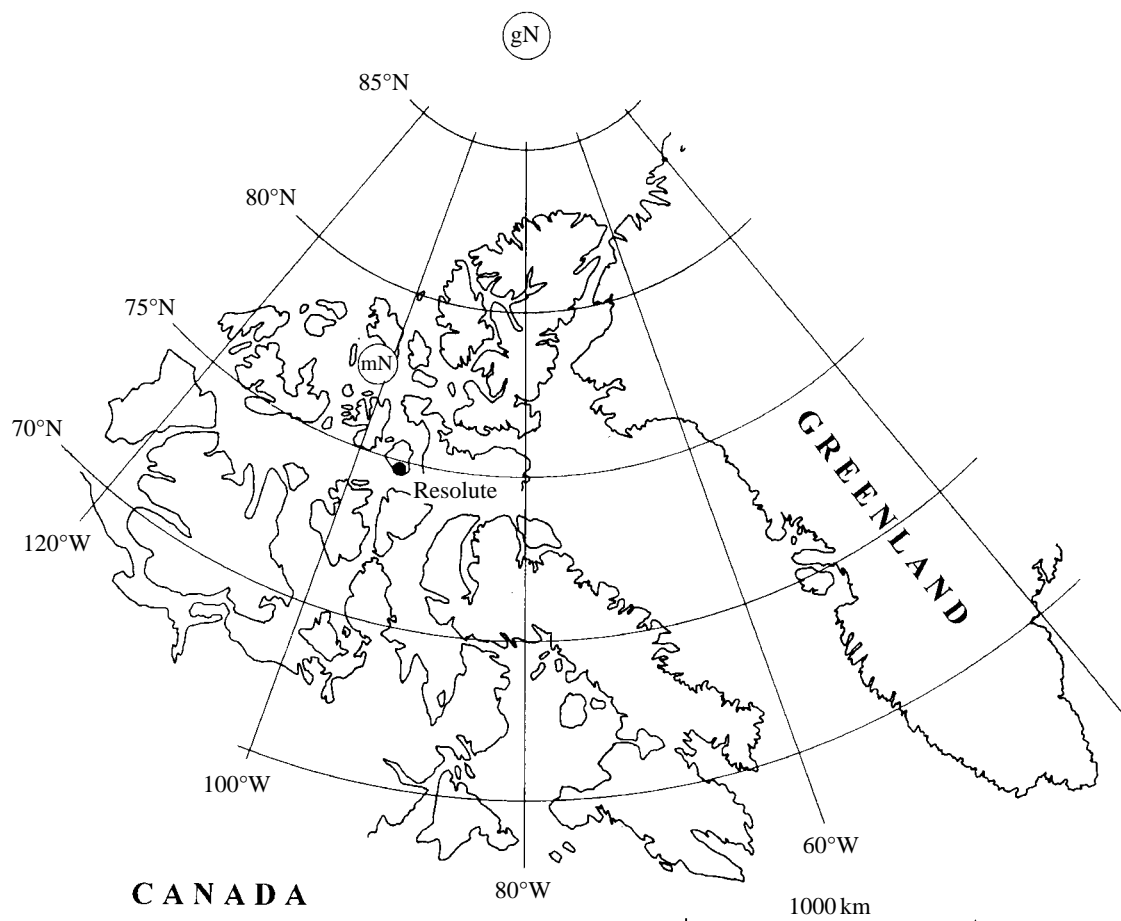


Fig. 1. Map of arctic Canada showing the locations of the geographic north pole (gN), the magnetic north pole (mN) and the study site in Resolute on Cornwallis Island (black dot).

Experimental procedure

Orientation tests were made by using modified 'Emlen funnels' (Emlen and Emlen, 1966) lined with typewriter correction paper (Tipp-Ex; see Rabøl, 1979; Beck and Wiltshko, 1981). The funnels were made of plastic, covered on top with a fine-meshed plastic net (allowing the birds to see the sky above) and fixed to a wooden bottom plate that could be opened to let the birds enter. With a top diameter of 300 mm and an inner height of 150 mm, the cage design allowed the birds to see approximately 160° of the sky centred around the zenith.

The local characteristics of the geomagnetic field during the test period (calculated mean values of variation data obtained at Resolute Bay magnetic observatory located within 1 km from the test site; L. R. Newitt, personal communication) were as follows: horizontal intensity (H) 1131 nT, vertical intensity (Z) 58 174 nT and total intensity (F) 58 191 nT. The local angle of inclination (I) was 88.9° and the declination angle (D) was approximately -46°. All values of magnetic parameters are necessarily approximate since the NMP moves continuously. The location of the NMP during 1992 was calculated to be slightly west of King Christian Island (78°30'N, 104°30'W), i.e. approximately 400 km from the study site in Resolute (L. R. Newitt, personal communication; see Fig. 1). Mean geomagnetic variation data for the study period are given in Table 1.

Snow buntings were tested for directional preferences under several different test conditions. (1) *Clear sunset skies* (maximum five-eighths cloud cover with the setting sun always clearly visible): (A) *control*, unmanipulated tests; (B) *polarized*, orientation cages were covered with linear dichroic polarizers (Plexiglas-laminated HN-38; Polaroid) with the E-vector oriented at -45° relative to the seasonally appropriate direction (for further details on polarizers, see Sandberg, 1988); (C) *depolarized*, double-layered pseudodepolarizers (Hostaphan; two sheets of 0.18 mm Hostaphan were stapled together with their fast axes oriented at 45°; degree of depolarization >90%) were placed on top of the funnels (for a full description of depolarization sheets, see Helbig, 1991) and (D) *clock-shifted*, the birds were kept in closed, artificially lit rooms for 5 days to shift their internal clock 4 h slow with respect to the natural day. (2) *Natural overcast* (more than six-eighths cloud cover, sun position not discernible by the human eye): (A) *control*, (B) *polarized* and (C) *depolarized*, as above. (3) *Simulated complete overcast* (cages were covered with a panel of 3 mm opaque diffusing Plexiglas to prevent the birds from seeing any celestial cues; for a full description of diffusers, see Sandberg and Pettersson, 1996): *control* only. Finally, in addition to the orientation cage experiments, we performed free-flight release experiments to study the directional behaviour of snow buntings under conditions that were as natural as possible. These experiments were performed at an airfield runway in an open area without any conspicuous topographical features nearby. We made two releases, one experiment under clear starry skies (zero-eighths cloud cover, no wind) and a second release test under complete overcast

Table 1. Mean geomagnetic variation during test hours as obtained at Resolute Bay magnetic observatory (within 1 km from the test site) in August 1992

Test date	Variation in x (nT)	Vector size (nT)	Variation in y (nT)	Vector size (nT)	Inclination (degrees)
11 August	100	641	210	-854	88.9
14 August	90	858	40	-835	88.8
15 August	120	704	80	-829	88.9
16 August	100	757	60	-832	88.9
17 August	50	709	20	-858	88.9
18 August	30	820	20	-874	88.8
19 August	140	717	70	-848	88.9
20 August	90	680	110	-821	89.0
21 August	160	703	120	-895	88.9
23 August	30	617	40	-843	89.0
24 August	110	617	30	-800	89.0
25 August	60	761	30	-849	88.9
26 August	50	789	200	-798	88.9
27 August	110	659	60	-844	88.9
28 August	20	741	50	-806	88.9
29 August	20	787	20	-855	88.9
30 August	40	775	20	-850	88.9
1-31 August	97	722	74	-832	88.9

Variation values, i.e. the difference between maximum and minimum values within the test hour, are given for x (north-south component of the geomagnetic field) and y (east-west component) in nanoteslas (nT). Corresponding absolute values of the vectors (in nT) are given for comparison.

Summary data (1-31 August) are based on mean values from between 21:00 and 24:00 h (covering the time interval when tests were performed) during the whole month.

(eight-eighths cloud cover, light northwest wind). The technique used was exactly the same as described by Sandberg *et al.* (1991) and Sandberg and Moore (1996).

Prior to each test, snow buntings were weighed, and fat deposits were estimated visually on the birds' abdomen and in the tracheal pit according to a seven-class scale, where no fat is equal to 0 and maximum fat corresponds to 6 (Pettersson and Hasselquist, 1985). Visual classification of subcutaneous fat is independent of body size and thereby avoids problems with mass-related variation caused by differences in gut, water and protein contents (Blem, 1990; Rogers, 1991; Kaiser, 1993). We recorded each individual as being lean (fat score ≤ 3) or fat (fat score ≥ 4) to check for any possible effect of body condition on the birds' orientation performance (Lindström and Alerstam, 1986; Sandberg, 1994; Sandberg and Moore, 1996).

Buntings were put into the orientation cages indoors approximately 20 min before local sunset with the funnels turned upside-down (to avoid scratches on the Tipp-Ex paper before the start of the experiment) and then carried to the test arena. Experiments started at sunset when the cages were returned to an upright position. Funnels were placed directly on the ground at specific sites which had been carefully

levelled. All experiments lasted for 1 h. Only young of the year were used in the orientation tests (aged according to Svensson, 1992).

Data analysis and statistics

Individual snow buntings were tested only once under each different experimental condition as described above (225 test hours/74 individuals, i.e. each individual participated on average in three different tests). The birds' activity patterns were registered as claw marks in the pigment of the Tipp-Ex paper and, after the completion of a test run, the papers were subdivided into 24 sectors and the claw marks crossing a certain line, passing through the majority of the registrations, were counted in each sector. On the basis of these activity distributions, a mean heading for each individual and test could be calculated by using standard procedures (Batschelet, 1981). We excluded bird-hours that either showed too little activity, with the minimum set at 50 registrations (16 tests excluded), or showed bimodal distributions (16 tests excluded). Mean headings were pooled for each separate experimental condition, resulting in sample mean vectors. Vanishing bearings of released snow buntings were treated in the same way, and a mean vector was calculated for each independent sample.

The Rayleigh test was applied to test for statistically significant directional preferences (Batschelet, 1981). Mean axes of orientation were chosen as the basis of analysis when the mean vector length resulting from doubling the angles (\mathbf{r}_2) was larger than the corresponding mean unimodal vector length (\mathbf{r}). Differences in mean angles between different test categories were examined by using the 'one-way classification test' (indicated by $F_{1,d}$; Mardia, 1972), and scatter around the mean direction, as given by vector lengths, was compared between samples by applying the 'test for the homogeneity of concentration parameters' (indicated by t ; Mardia, 1972). If one or both of the samples involved was randomly distributed or bimodal, or if the vector lengths were significantly different from each other, the Watson's U^2 -test (indicated by U^2) was used (Batschelet, 1981).

Results

Fat birds comprised 37.5% of the total number of snow buntings tested during the early part of the experimental study period (11–20 August) and 23.9% during late tests (21–30 August). A check for possible seasonal effects failed to reveal any statistically significant differences in directional selections between early and late tests in any of the test categories discussed below (clock-shift and simulated complete overcast tests were run only during the late part of the season).

Orientation under clear skies

Snow buntings tested in the near-vertical geomagnetic field at Resolute, under clear twilight skies (control), selected a mean direction towards geographic northwest (magnetic north), close to the sunset azimuth (Fig. 2, top left). When this data set was subdivided into lean (fat classes 0–3) and fat (fat

classes 4–6) birds, lean birds chose a northerly mean direction which was significantly different from the sunset azimuth (95% confidence interval: $\pm 27^\circ$; Fig. 2, middle left). Fat birds, in contrast, preferred a southwesterly mean direction, significantly different from the position of the setting sun (Fig. 2, bottom left) and significantly different from the mean direction of lean birds ($F_{1,26}=21.2$, $P<0.001$).

Buntings which viewed the sky through sheets of polarizers that experimentally shifted the E-vector direction 45° to the left of its normal alignment displayed a slightly more concentrated mean direction compared with controls, but with a closely similar northwesterly directionality (Fig. 2, top middle). Lean birds oriented along a mean direction that was virtually indistinguishable from the total sample (Fig. 2, middle centre), mainly because of the small number of fat birds (Fig. 2, bottom middle) tested under this condition. The orientation behaviour of the few fat birds does not allow any meaningful analysis, but the directional tendency agrees with that of fat controls.

When snow buntings were exposed to almost completely depolarized skylight (see Materials and methods), they selected a mean direction towards the west (Fig. 2, top right), which was significantly different from the sunset azimuth (compare control and polarized conditions). However, the mean direction was not significantly different from those of the control and polarized groups. Inspection of the orientation behaviour of lean and fat birds under these conditions (Fig. 2, middle and bottom right) revealed a statistically significant difference in mean direction between these two categories ($F_{1,25}=12.1$, $P<0.01$). This difference between fat and lean individuals closely resembles the corresponding differences obtained for the control birds.

Twenty snow buntings were subjected to an experimentally shifted light:dark regime where their internal clock was set 4 h behind normal time. As shown in Fig. 3 (top), the birds failed to show a significant mean direction and, if anything, there was a tendency to orient in a direction opposite to the expected direction (predicted direction = mean direction of controls + $4 \times 15^\circ = 309^\circ + 60^\circ = 9^\circ$). Lean clock-shifted buntings showed a southerly mean direction (Fig. 3, middle) almost opposite to the expected direction (48°), whereas fat birds displayed a directional tendency (not statistically significant; Fig. 3, bottom) that agreed reasonably well with expectations compared with fat controls (expected direction 292°). The mean direction of lean clock-shifted birds was significantly different from the corresponding lean control direction ($F_{1,27}=24.0$, $P<0.001$).

Orientation under overcast

The directions of the control birds tested under natural overcast conditions were randomly distributed (Fig. 4, top left). Although the results for the subsample of lean snow buntings were less scattered, they still failed to show a significant mean direction (Fig. 4, middle left, $P>0.05$). The easterly distribution of headings shown by lean birds was significantly different from that of lean controls tested under

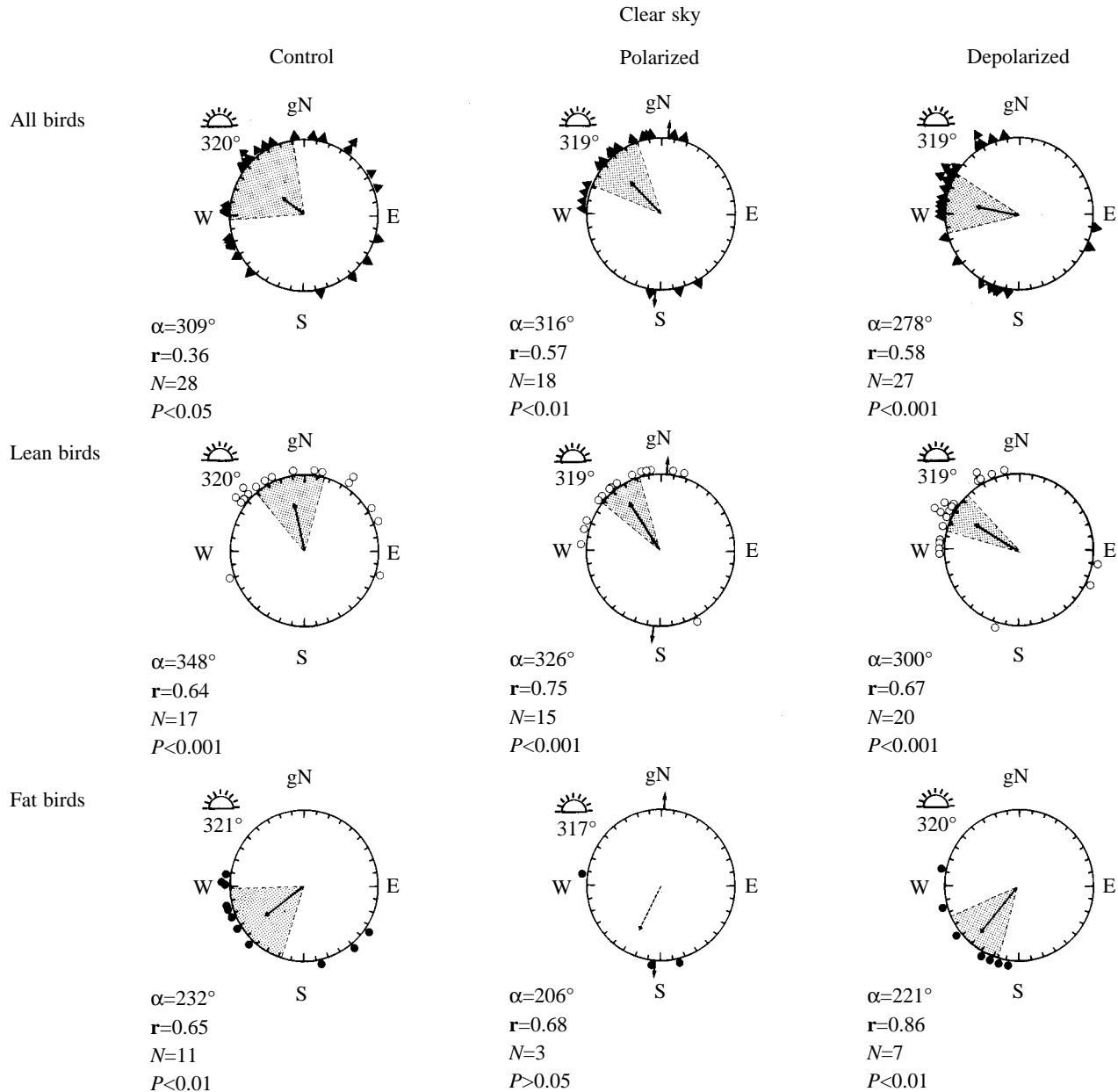


Fig. 2. Autumn orientation of snow buntings (*Plectrophenax nivalis*) under clear sunset skies at Resolute in the Canadian Arctic, approximately 400 km away from the magnetic north pole (NMP). The left-hand column shows the result of unmanipulated control experiments, the middle column shows the orientation behaviour of the birds when the polarizer E-vector direction was shifted 45° counterclockwise from normal, and in the right-hand column results from tests where incoming light was depolarized are illustrated. All tests were run in the local near-vertical magnetic field. Top row diagrams show the summary results for the three test categories, the middle and bottom rows display the results when subdivided into lean and fat individuals, respectively. The mean sunset azimuth in the middle of the test hour is indicated outside each circular diagram. Similarly, the direction towards geographic north (gN= 360°) is shown. Magnetic declination was approximately -46° (=geographic 314°). Arrows outside the diagrams in the middle column indicate the alignment of E-vectors. Each triangle/circle on the periphery of the diagrams represents the mean heading of one individual. Open and filled circles denote lean and fat birds, respectively. The mean vector (α) of each sample is illustrated by an arrow surrounded by the 95% confidence interval (shaded) in cases of statistical significance. Arrow lengths are proportional to the mean vector length (r) and are drawn relative to the radius of the circles (radius=1). Significance levels (P) are according to the Rayleigh test (Batschelet, 1981).

clear skies ($U^2>0.2$, $P<0.05$). Fat birds oriented in almost exactly the same direction as the corresponding category tested under clear skies, with a well-defined southwesterly mean

direction (Fig. 4, bottom left) that was significantly different from the direction obtained for lean individuals under overcast conditions ($U^2=0.3$, $P<0.01$).

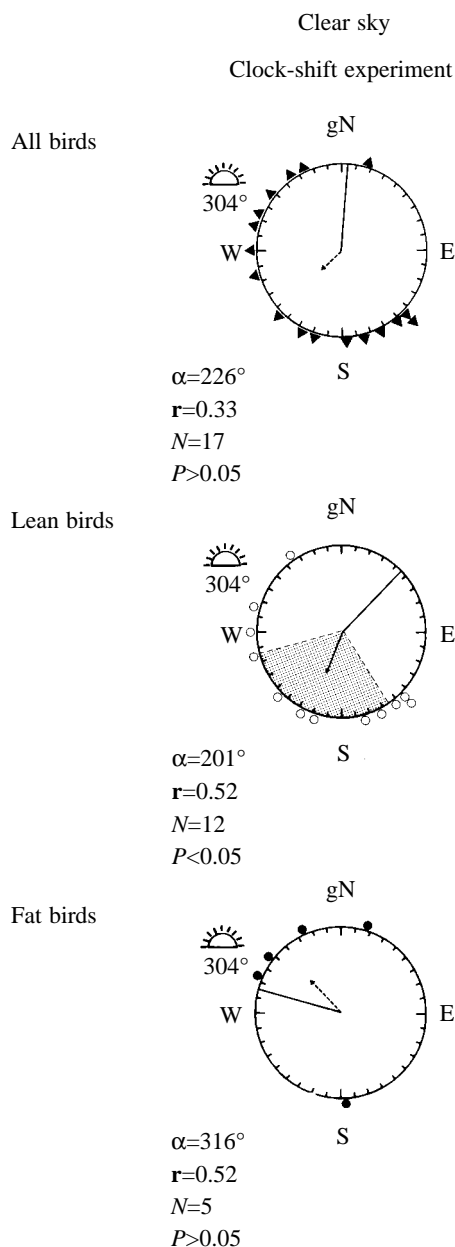


Fig. 3. Directional choices of snow buntings (*Plectrophenax nivalis*) subjected to a 4 h slow clock-shift relative to the natural day. Solid lines inside the circles denote the expected mean directions based on the treatment. See legend to Fig. 2 for further details.

When the orientation cages were covered with polarizers under overcast conditions, an otherwise absent solar cue was experimentally introduced and incoming skylight was polarized along one axial E-vector direction only. Under this condition, snow buntings chose a northnorthwesterly direction which approximately coincided with the northern end of the polarization axis (Fig. 4, top centre). This mean direction was significantly different from the circular distribution of control headings ($U^2>0.2$, $P<0.05$). The subdivided sample revealed that lean birds also oriented northwards, even closer to the

northern end of the polarization axis (Fig. 4, middle centre), whereas fat individuals displayed a non-significant axial distribution along the polarization axis (Fig. 4, bottom centre). Fat birds were significantly more scattered in their choices of headings than were lean birds ($t=2.2$, $P<0.05$).

In the local near-vertical geomagnetic field, under natural overcast and with the incoming skylight being depolarized by more than 90 %, the snow buntings became disoriented (Fig. 4, top right). The distribution of the total sample was significantly different from that in the corresponding polarized tests ($U^2=0.2$, $P<0.05$), but not from that of the control birds. The directions of lean birds were less scattered, but the axial directional tendency failed to reach significance by the Rayleigh test (Fig. 4, middle right). However, the sample containing fat individuals showed a significantly directed mean orientation towards eastsoutheast (Fig. 4, bottom right) with a significantly different distribution of headings compared with that of lean birds ($U^2=0.2$, $P<0.05$).

In addition to tests run under natural overcast, a series of control experiments was performed under simulated complete overcast (see Materials and methods). The results are shown in Fig. 5. All three samples (total, lean and fat) were significantly axially distributed, which sets them apart from the results obtained under natural overcast. The total sample shows orientation along a north–south axis (top), lean birds along a northnorthwest–southsoutheast axis (middle) and fat birds along an approximate northeast–southwest, axis which was significantly different from the corresponding orientation for lean birds (non-overlapping confidence intervals). Fat birds were also significantly unimodally oriented, with a mean orientation of 236° ($P\leq 0.05$, compare fat controls under natural overcast), but with $r<0.2$.

Free-flight release experiments

Two free-flight release experiments were performed at the end of the experimental period. First, 20 birds were released under completely clear starry skies, but only three individuals took off on migratory flights (mean direction $\alpha=151^\circ$, $r=0.95$, $N=3$, $P<0.07$). It should be noted that these 20 birds consisted of the clock-shifted group, i.e. they had participated in orientation cage tests on the evening before the release. As shown in Fig. 6, snow buntings that were released under complete overcast oriented towards southsoutheast with very little scatter around the mean direction. Unfortunately, these birds were not checked for their fat levels before the experiment. However, at the latest fat scoring before this test (1–3 days earlier), no bird had less than fat score 3.

Possible influence of variation in the geomagnetic field

Given the fact that snow buntings were able to orient even in the absence of visual cues (natural overcast and simulated complete overcast, see above), we investigated the possibility that the naturally occurring variability in the two most relevant geomagnetic field components (x and y , see Table 1)

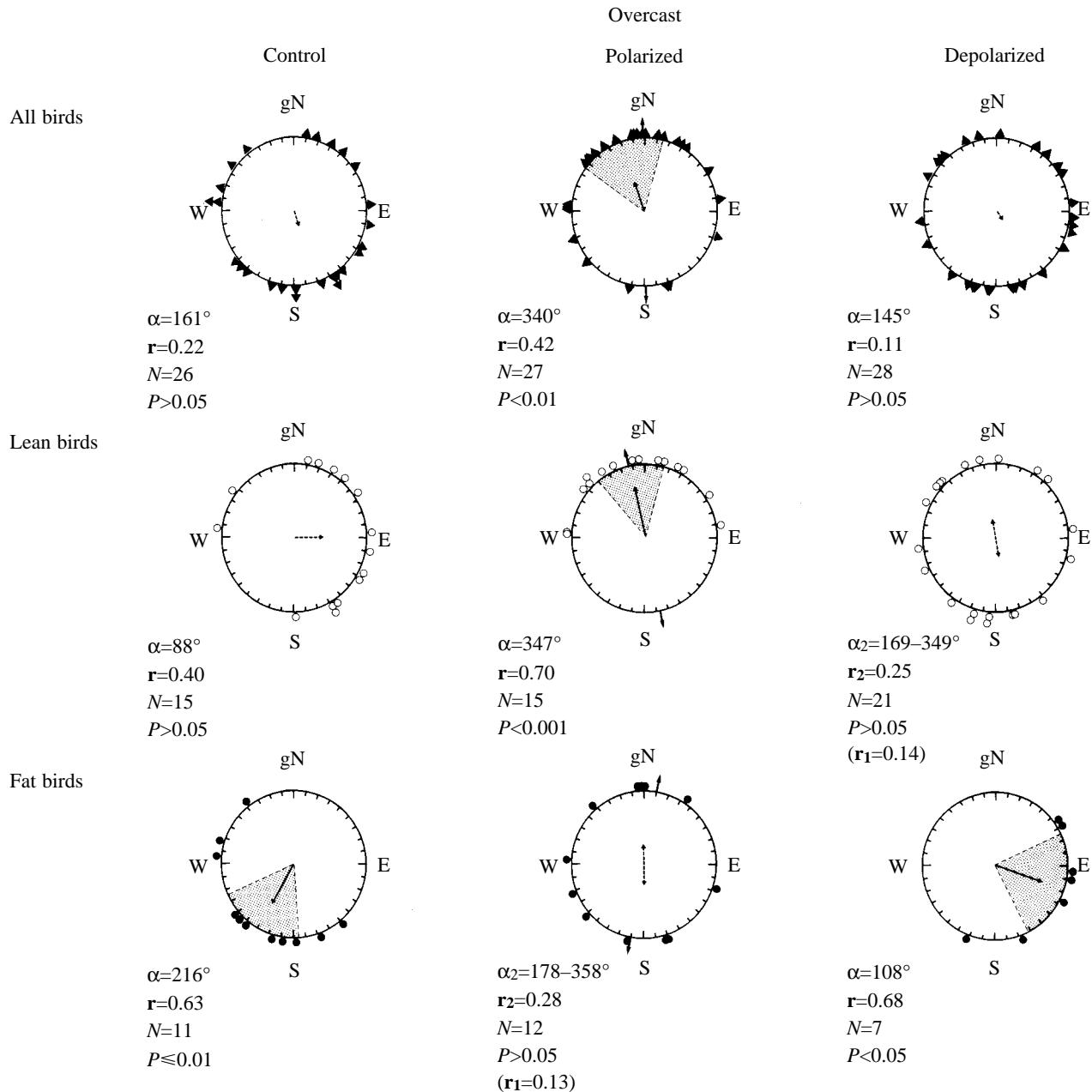


Fig. 4. Mean orientation of snow buntings (*Plectrophenax nivalis*) under natural overcast skies. When the mean vector length resulting from doubling the angles (r_2) was larger than the corresponding mean unimodal vector length (r_1), mean axes of orientation (α_2) were chosen as the basis of analysis and single-ended arrows were replaced with double-ended arrows. In these cases, unimodal vector lengths (r_1) are given for comparison. Other details are as in Fig. 2.

might have influenced the orientation behaviour of the birds. Concerning directional selections, we first classified the birds into north-seeking ($271-90^\circ$) and south-seeking ($91-270^\circ$) individuals. There was no significant difference between natural overcast and simulated complete overcast conditions ($\chi^2=0.2$, d.f.=1, $P>0.5$), thus allowing us to pool these two categories. We performed a binary stepwise logistic multiple regression of the x and y vector values (see Table 1) against directional choices and failed to find any statistically

significant relationships, i.e. body condition was the only evident predictor of directional selections of snow buntings (see above). However, the concentration of individual headings (r) was significantly negatively correlated with magnetic variation in both the x and y components (stepwise multiple regressions; x -component, $F_{1,46}=9.442$, $P<0.005$; y -component, $F_{1,46}=6.043$, $P<0.02$), thus indicating an influence of geomagnetic variability on the ability to maintain preselected headings.

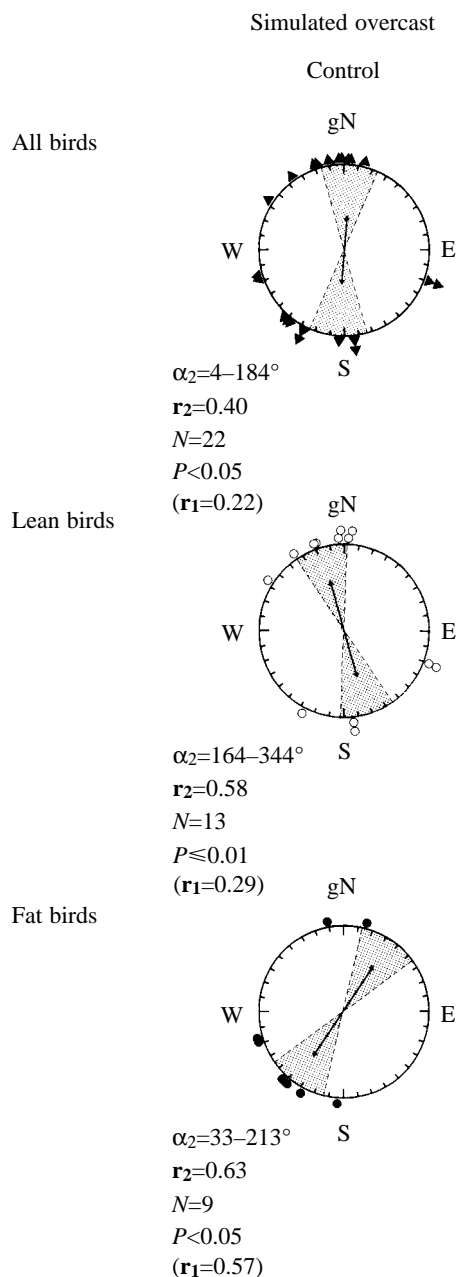


Fig. 5. Autumn orientation of snow buntings (*Plectrophenax nivalis*) under simulated complete overcast. Confidence intervals for bimodal distributions are according to Prentice (1984). For further details, see Figs 2 and 4.

Discussion

Orientation of snow buntings close to the NMP

So far, all investigations concerning the existence and use of a magnetic compass in migratory bird species have been performed in artificially produced magnetic fields where the direction towards magnetic north and/or the inclination angle I of the field lines have been experimentally manipulated (for a review, see Wiltschko and Wiltschko, 1995). For example, birds have often been tested in artificial vertical fields

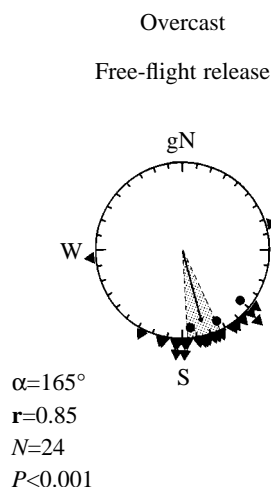


Fig. 6. Vanishing directions of migrating snow buntings (*Plectrophenax nivalis*) released under complete natural overcast (symbols outside the periphery). Dots inside the periphery indicate the vanishing directions of three individuals successfully released under clear skies (not included in the calculated mean values). Further details are as in Fig. 2.

($I=88-90^\circ$) to evaluate the potential importance of magnetic cues relative to directional information from celestial cues such as the sun, skylight polarization patterns and stars. To our knowledge, the present study constitutes the first attempt to examine the orientation behaviour of a migratory bird in a natural near-vertical ($I>88^\circ$, see Materials and methods) geomagnetic field.

Recently, orientation tests in southeast Sweden showed that snow buntings are capable of detecting and using the geomagnetic field for their orientation. Furthermore, it seemed that the buntings rely primarily on their magnetic compass for orientation while on passage migration through temperate-zone areas (Sandberg and Pettersson, 1996). Because snow buntings breed in the high Arctic regions of Canada, close to the NMP, they were chosen as the most suitable test subjects in investigations of orientation performance in a natural near-vertical geomagnetic field. At our test site in Resolute, the stars do not become visible until around mid-August, i.e. young snow buntings are likely to grow up without access to either geomagnetic or stellar directional information. According to present knowledge, the only remaining option available for the development of a functional compass would be the use of celestial rotation of daytime (solar) cues during ontogeny. At least two visual cues may be used to assess celestial rotation: the sun's path across the sky and the associated skylight polarization patterns (Brines, 1980; Brines and Gould, 1982; Phillips and Waldvogel, 1982, 1988).

Orientation of snow buntings under clear skies

When snow buntings were tested under the clear-sky control condition, they selected a seasonally aberrant northwesterly mean direction. However, the orientation of migratory activity

differed significantly between lean and fat birds, the latter showing a more appropriate southwesterly directional preference. This agrees well with the results of several recent studies which have emphasized the importance of energetic status for the directional selections of both nocturnal and diurnal migrants (e.g. Lindström and Alerstam, 1986; Sandberg, 1994; Sandberg and Moore, 1996; Bäckman *et al.* 1997). Individuals that have not yet reached an appropriate level of body condition for impending migratory flights tend to either be inactive (stay at their current location) or to reorient in more or less opposite directions relative to the expected migration route (presumably in search of better refuelling areas; see Alerstam, 1978).

Snow buntings that were exposed to an experimentally shifted direction of the band of maximum polarization did not respond in any obvious way to the treatment. The same was true for birds that were tested in the absence of polarized light cues (depolarized). Instead, the results suggest that the three different groups of birds tested under clear sky conditions based their orientation on common directional information. The similarity in behaviour between test categories further strengthens the conclusion that body condition seems to be of crucial importance for the choice of direction. What then is the underlying source of directional information? At this point, it is difficult to see any alternative other than the sun azimuth as the basis of directional selections. This seems to be at odds with results presented for other migrants. Although visual information at sunset has been shown to be of primary importance for the orientation of several species of night migrants (see Moore, 1987), most studies so far report that polarized skylight patterns, rather than the sun itself, provide the relevant cue information during migration (e.g. Able, 1982, 1989; Helbig, 1990, 1991; Phillips and Moore, 1992) as well as during ontogenetic development (Able and Able, 1993, 1995).

Our results do not preclude the possibility that skylight polarization is used to calibrate the sunset position during ontogeny but, if this is the case, then the failure of snow buntings to respond to the experimental manipulation under both polarized and depolarized conditions suggests that the roles of the two solar cues might be reversed during the migration phase. This shift in relative importance between cues during ontogeny and actual migration has been reported for several species of migratory bird where celestial rotation of both night and day skies calibrates the magnetic compass during ontogeny (for a review, see Wiltschko and Wiltschko, 1991), whereas wild birds caught during migration seem to pay more attention to geomagnetic information and even recalibrate their celestial compasses (stellar and sun) using magnetic directions (e.g. Wiltschko and Wiltschko, 1975a,b, 1976).

The clock-shift experiment resulted in a non-significant circular distribution, with the majority of headings well away from the expected direction. Together with the fact that the directional tendency of clock-shifted birds did not differ significantly from the mean direction of clear-sky controls, this seems to indicate that young snow buntings may use the sunset

azimuth as a fixed reference. This corresponds to the findings obtained by Moore (1980), who tested Savannah sparrows (*Passerculus sandwichensis*) subjected to a 6 h slow clock-shift and concluded that these birds seemed to orient at a constant angle relative to the sunset position. Katz (1985) reached the same conclusion for autumn-migrating robins (*Erithacus rubecula*) on the basis of a seasonal shift in orientation corresponding to the shift in sunset azimuth. However, in a later study on spring-migrating robins, Helbig (1991) managed to find predictable responses to both fast and slow clock-shift regimes, thus indicating that robins do take into account the dial movement of the sun's position. Previous data obtained in clock-shift experiments tend to suggest that the experience (age) of the birds may be a crucial factor for the establishment of a time-compensated sun compass. To our knowledge, all attempts to clock-shift autumn-migrating birds (presumably young birds) have failed, whereas the majority of spring experiments (experienced birds) have yielded positive results (Wiltschko *et al.* 1997). For example, young starlings (*Sturnus vulgaris*) did not react to a 6 h clock-shift during their first autumn migration period, but by the end of the following spring migration season they showed the expected shift in direction when exposed to an identical clock-shift, suggesting that the time-compensated sun compass develops through a learning process based on an underlying reference system (Wiltschko, 1980).

Inspection of the behaviour shown by lean and fat birds reveals that it was the lean birds that were mainly responsible for the apparent lack of response to the clock-shift treatment. The southwesterly mean direction of lean birds is puzzling; it is almost exactly opposite to the expected direction based on the clock-shift treatment. Furthermore, the mean direction is indistinguishable from that of *fat* control, polarized and depolarized groups. Hence, at this point, we can only speculate that the consistency in orientation behaviour shown by all experimental categories except the clock-shifted birds perhaps indicates that there was some unknown effect of the treatment. This may also be supported by the extremely low success rate obtained in the free-flight release experiment performed with the clock-shifted birds (only three birds out of 20 took off on flights). Thus, we cannot conclude that young, inexperienced snow buntings lack a time-compensated sun compass and, therefore, this question must remain open.

Orientation of snow buntings under overcast

While planning orientation experiments under overcast skies in the near-vertical geomagnetic field, we assumed that snow buntings would be unable to orient their activity in an appropriate migratory direction and that their directional behaviour would be independent of body condition. This should at least be true for control (both natural and simulated complete overcast) and depolarized groups. If, however, the buntings were able to use skylight polarization for their orientation, then the polarized sample should become axially distributed (no known auxiliary cue available to discriminate between the two ends of the polarization axis).

The outcome of overcast tests followed predictions to a certain extent, i.e. the total and lean groups of control and depolarized birds became randomly distributed. However, polarized birds, and especially the lean group, somehow managed to select one specific end of the introduced E-vector axis. This relatively consistent directional choice is surprising and difficult to explain given the assumed absence of geomagnetic information. Equally astounding was the orientation performance of fat buntings tested under control and depolarized conditions. First, fat controls were obviously able to select a southwesterly mean direction almost identical to that of fat controls tested under clear skies. How was this possible? Since natural overcast was defined as more than six-eighths of cloud cover with the sun position invisible to the human eye, we cannot rule out the possibility that the few very limited patches of blue sky (three out of six tests only) may have contained enough visual information from polarized light cues to enable the snow buntings to orient towards southwest (but see below). If we consider this possibility, the mean axial direction of the E-vector was approximately northeast–southwest, which means that fat controls must still have been able to select the ‘correct’ end of the polarization axis (compare lean polarized birds). Second, the relatively small sample of fat snow buntings that were tested under overcast in the absence of polarized light cues oriented towards east-southeast. In spite of the few individuals tested and the fact that one sample out of 20 will yield a significant result by chance alone (see Batschelet, 1981), we find it interesting to note that the mean direction roughly coincides with magnetic south. Finally, the free-flight release experiment clearly showed that snow buntings are able to select a well-defined southerly migratory direction even under complete natural overcast.

Tests conducted under simulated complete overcast conditions were intended to act as controls for the corresponding natural overcast experiments, i.e. to rule out any possibly confounding variables such as unforeseen gaps in the cloud cover during tests, movement of clouds across the sky and possible effects of wind. To our surprise, the snow buntings were significantly oriented even under this restricted condition. The total sample shows a bimodal distribution along an approximate north–south axis with approximately half of the lean birds heading towards north-northwest, while most fat birds selected southwesterly directions. These results are interesting (1) because the diffusers should have prevented the birds from using any visual cues, (2) because the near-vertical local geomagnetic field should have precluded the use of magnetic information, and (3) because of the unexpected similarity between these tests and the clear-sky control tests (compare fat and lean samples).

Orientation tests in artificially produced vertical magnetic fields with snow buntings on passage migration through southeast Sweden showed an axially bimodal response under clear skies and a random distribution under simulated complete overcast (Sandberg and Pettersson, 1996). Bimodal distributions were recorded in several experiments when

birds were tested in vertical magnetic fields under clear skies. For example, Bingman and Wiltschko (1988) used spring-migrating dunnocks (*Prunella modularis*) in outdoor experiments and found that the dunnocks displayed an axial response in a 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 magnetic field onto some visual cue(s). A similar information transfer was indicated in orientation experiments with wheatears (*Oenanthe oenanthe*) (Sandberg *et al.* 1991). However, there were no indications of such an information transfer in the study on snow buntings tested in southeast Sweden. Furthermore, both the aforementioned wheatears and snow buntings became disoriented when tested in vertical magnetic fields under simulated complete overcast (see Sandberg *et al.* 1991; Sandberg and Pettersson, 1996; see also Åkesson, 1994).

Why then did the snow buntings tested close to the NMP not become disoriented under overcast conditions? What is the underlying basis for their orientation performance? We can only speculate that the sole information source available, however unlikely, is the geomagnetic field. The fact that the concentration of individual headings was negatively correlated with the variation in both the *x*-component (north–south) and the *y*-component (east–west) of the geomagnetic field suggests an involvement of magnetic cues in the maintenance of preselected bearings. Furthermore, it has been shown that the magnetic compass of birds is narrowly tuned to the total intensity of the ambient magnetic field within approximately $\pm 25\%$ (Wiltschko, 1978). In addition, this functional window can be enlarged to encompass field strengths both lower and higher than those found on Earth. It appears that exposure to a given intensity for a certain period is sufficient for adaptation to new magnetic circumstances. Does growing up close to the NMP enable birds to extract directional information even from such an extreme set of geomagnetic parameters? Sandberg *et al.* (1991) showed that wheatears are able to use their magnetic compass in west Greenland, where the inclination is as steep as 81° . What is the angular limit of a functional inclination compass? Does exposure to a near-vertical magnetic field during ontogenetic development enable birds to discriminate between polewards and equatorwards even when *I* exceeds 88° ?

Concluding remarks

The data presented in this paper show that snow buntings that are ready to migrate, i.e. individuals that have deposited adequate energy stores, are able to select seasonally appropriate directions in a near-vertical geomagnetic field close to the NMP. This ability seems to be independent of access to visual orientation cues. Without reverting to some unknown cue(s), the only remaining source of directional information is the geomagnetic field. If snow buntings are able to orient magnetically 400 km from the NMP, which parameter of the geomagnetic field is the most likely information source?

Although the angular limit of the inclination compass is unknown, it appears highly unlikely that the birds could discriminate between an inclination angle of approximately 89° and the true vertical (90°). However, Rodda (1984), when analysing his data on young homing alligators (*Alligator mississippiensis*) with respect to magnetic parameters, found a significant correlation between the directions chosen by the alligators and minute changes in the angle of inclination in the region of 0.001° . If snow buntings have a comparable discrimination ability, perhaps connected to their long exposure to the near-vertical field during ontogenetic development, then it might be possible for these birds to use an inclination compass. Clearly, further investigations concerning the angular limit of the magnetic inclination compass are needed, especially during ontogenetic development.

We wish to thank Thomas Alerstam and Gudmundur Gudmundsson for critically reading an earlier version of this paper. Claudia Pfabe skilfully participated in the field work. Björn Holmquist provided help with statistics whenever we needed it. Larry Newitt kindly supplied geomagnetic data from Resolute Bay magnetic observatory. Furthermore, we thank Steffi Douwes for drawing the figures. This study was performed as a Polar Continental Shelf Project (PCSP no. 218-92) with logistical support supplied by PCSP. It was a joint project between the Bird Migration Research Group at Lund University and Ottenby Bird Observatory. Financial support was received from the Swedish Natural Research Council (to R.S.), Stiftelsen Ymer-80, the Swedish Ornithological Society (G. Danielsson's foundation), Uddenberg-Nordingska Stiftelsen, Stiftelsen Olle Engkvist Byggmästare and Ottenby Bird Observatory (financial account). This is report no. 164 from the Ottenby Bird Observatory.

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