

SANDERLINGS (*CALIDRIS ALBA*) HAVE A MAGNETIC COMPASS: ORIENTATION EXPERIMENTS DURING SPRING MIGRATION IN ICELAND

GUDMUNDUR A. GUDMUNDSSON^{1,2} AND ROLAND SANDBERG^{1,*}

¹Department of Animal Ecology, Lund University, Ecology Building, SE-223 62 Lund, Sweden and

²Icelandic Institute of Natural History, PO Box 5320, IS-125 Reykjavik, Iceland

*Author for correspondence (e-mail: Roland.Sandberg@zoekol.lu.se)

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Summary

The migratory orientation of sanderlings (*Calidris alba*) was investigated with cage experiments during the spring migration in southwest Iceland. Sanderlings were exposed to 90° counterclockwise-shifted magnetic fields under both clear skies and natural overcast. Clear sky control tests resulted in a northerly mean direction, in agreement with predictions based on ringing recovery data and earlier visual observations of departing flocks. Sanderlings closely followed experimental deflections of magnetic fields when tested under clear skies. Control experiments under natural overcast resulted in a bimodal distribution approximately coinciding with the magnetic north–south axis. Overcast tests did not reveal any predictable response to the experimental treatment, but instead resulted in a non-significant circular distribution. The time of orientation experiments in relation to the tidal cycle affects

the motivation of the birds to depart, as shown by the lower directional scatter of headings of individuals tested within the appropriate tidal window under clear skies. Sanderlings were significantly more likely to become inactive under overcast conditions than under clear sky conditions. The results demonstrate, for the first time, that a wader species such as the sanderling possesses a magnetic compass and suggest that magnetic cues are of primary directional importance. However, overcast experiments indicate that both celestial and geomagnetic information are needed for sanderlings to realize a seasonally appropriate migratory orientation.

Key words: shorebird, migration, orientation, geomagnetic field, *Calidris alba*, sanderling.

Introduction

Research on the orientation system of migratory birds has produced an impressive amount of information concerning which directional references migrants are able to use during their journeys between breeding and wintering areas. Today, it is widely accepted that birds integrate directional information from several different environmental sources, e.g. the azimuth of the sun, the rotation centre of the starry sky and the inclination of the geomagnetic field (for reviews, see Berthold, 1991; Papi, 1992; Wehner et al., 1996). Although much is known about the capacity of migrants to use different kinds of directional information, the available data are based on experiments involving relatively few species. For example, only 18 migratory bird species, all of them passerines, have been shown to use a magnetic compass (Wiltschko and Wiltschko, 1995). In addition, there appears to be significant diversity as regards the relative importance of different cues during migration (for a review, see Wiltschko et al., 1997) and during the ontogenetic development of compass mechanisms (Able and Able, 1990; Weindler et al., 1996, 1998). The taxonomic scope of orientation studies so far has been severely restricted.

Although our present knowledge of migratory orientation mechanisms is based largely on cage experiments with

nocturnally migrating passerines, the most accurate information about actual migration routes, including specific stopover sites, originates from studies on non-passerine birds. Analyses of ringing recoveries, direct visual observations, radar studies and recent satellite telemetry on waterfowl (Alerstam et al., 1986, 1990; Gudmundsson et al., 1995), seabirds (Jouventin and Weimerskirch, 1990), raptors (Kjellén et al., 1997) and waders (e.g. Richardson, 1979; Alerstam et al., 1986, 1990; Gudmundsson, 1994; Alerstam and Gudmundsson, 1999) have given detailed accounts of migration tracks that allow evaluations of the possible compass mechanisms involved in orientation.

Waders are renowned for their spectacular, long-distance migrations between high Arctic breeding grounds and wintering areas in the southern hemisphere (e.g. Morrison, 1984; Dick et al., 1987; Wymenga et al., 1990). On their journeys, which sometimes involve non-stop flights of thousands of kilometres across ecological barriers such as the open sea, the birds will have to cope with extreme variability in orientation cue availability. For example, while migrating through Arctic regions, birds may face difficulties with the steep inclination of the geomagnetic field that can render the

magnetic compass unreliable or even unusable, 24 h daylight during summer that makes the star compass useless after passage through the Arctic circle on spring migration and, finally, the compression of longitudes, which may introduce problems in using the time-compensated sun compass, particularly during rapid east–west flights (Alerstam, 1990; Alerstam et al., 1990; Sandberg et al., 1991, 1998; Gudmundsson and Alerstam, 1998). Furthermore, when crossing the magnetic equator region, the magnetic inclination compass will become inoperative (e.g. Wiltschko and Wiltschko, 1995; Sandberg and Holmquist, 1998).

Shorebirds show a high degree of site faithfulness, not only to breeding and wintering sites, but also to staging areas along the migration route (Pienkowski, 1976; Smith and Houghton, 1984; Evans and Townshend, 1988). Recurrence rates at stopover sites are much higher than for passerines (Nisbet, 1968). The life-span of waders is much longer than that of passerines (e.g. Myers, 1980). Taken together, these extraordinary features of the migratory flights and life history characteristics of waders make them highly interesting as test subjects in carefully controlled cage experiments designed to elucidate the orientation mechanisms that enable shorebirds to perform their annual migrations.

Despite our detailed knowledge about the migration systems of waders, we are aware of only two successful attempts to study experimentally the orientation behaviour of waders in orientation cages. First, Sauer (1963) performed cage trials with a small group of hand-raised Pacific golden plovers (*Pluvialis dominica fulva*) and found that these birds were well oriented when they had access to celestial cues, but became disoriented under complete overcast. Second, Sandberg and Gudmundsson (1996) tested autumn-migrating dunlins (*Calidris alpina*) in Iceland whose orientation behaviour in 'Emlen funnels', under clear sky conditions, corresponded very well with the migratory direction predicted from ringing recovery data. In spite of the fact that it is clearly possible to measure experimentally the directional behaviour of shorebirds, investigations of the relative importance of different orientation cues used by non-passerines are completely lacking.

The aim of our study was, for the first time, to examine the relative importance of celestial and magnetic cues in the migratory orientation of a shorebird species. As test subjects, we chose the sanderling (*Calidris alba*) on spring migration through Iceland. We tested sanderlings in the local unmanipulated geomagnetic field and in experimentally deflected magnetic fields under both clear and overcast skies. The results are compared both with available ringing recovery data and with an earlier observational study on vanishing directions of departing sanderling flocks (Gudmundsson and Lindström, 1992).

Materials and methods

Test birds and study site

Sanderlings (*Calidris alba* L.) have a high Arctic breeding distribution. Three centres of breeding have been suggested:

the Canadian Arctic, northeast Greenland and Taymyr in Siberia (Cramp and Simmons, 1983; Meltofte, 1985; Godfrey, 1986; Summers et al., 1987). During the winter, sanderlings can be found scattered along most temperate and tropical coasts of the world (Cramp and Simmons, 1983; Morrison, 1984; Smit and Piersma, 1989).

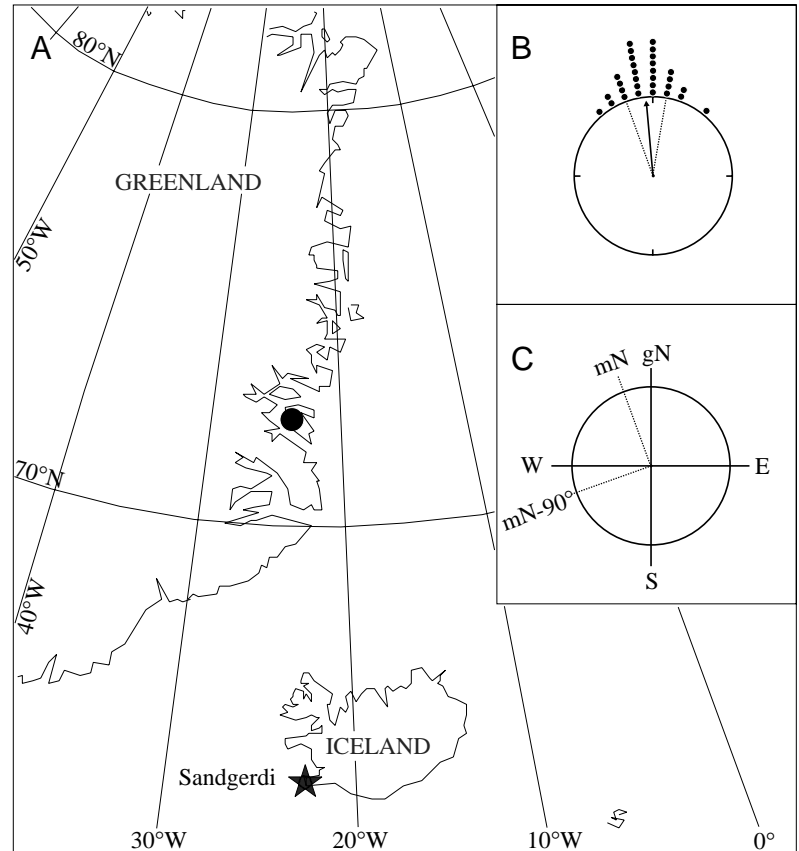
The present series of orientation cage experiments was performed at a stopover site in southwest Iceland (Fig. 1), Sandgerdi (64°03'N, 22°43'W), between 23 May and 1 June in 1996–1998. Waders, mainly sanderlings, were caught on the local shores using a cannon-net set at locations where sanderling roosts had been observed previously. Captured birds were ringed, measured (wing length and total head plus bill to the nearest mm), weighed (to the nearest g) and aged on the basis of plumage characteristics (wing coverts; Prater et al., 1977). The birds were kept for a short time only, on average 4.7 h (range 2–11 h), in wooden holding cages until tested later the same evening.

Equipment and test protocol

Orientation experiments were conducted by using modified 'Emlen funnels' (Emlen and Emlen, 1966) lined with typewriter correction paper (Tipp-Ex; see Beck and Wiltschko, 1981). The funnels were made of aluminium and were covered with a fine-meshed plastic net that allowed the test birds to see a minimum of 130° of the sky overhead (for a detailed description of the funnels, see Sandberg and Gudmundsson, 1996). We manipulated the local geomagnetic field by using pairs of magnetic coils (quadratic cross section 1.2 m × 1.2 m, clearance between coils in a pair 1.2 m). Coil formers (20 mm × 20 mm) were made of aluminium and wound with 140 turns (672 m) of insulated copper wire (1.18 mm diameter, 15.63 Ω km⁻¹). The power supply was a 12 V car battery, and the current was held constant by a regulator to ensure homogeneous fields. At the position of the orientation cage, the calculated homogeneity of the artificial field shows that the maximum deviation in total field intensity was less than 3% along the coil axis and less than 2% perpendicular to this axis (J. Bäckman, personal communication). By orienting such a pair of coils along a magnetic southwest/northeast axis, magnetic north could be deflected 90° counterclockwise from its normal position. The local characteristics of the geomagnetic field were as follows: declination -21° (magnetic north=geographic 339°); inclination +75°.

Sanderlings were tested for their directional preferences under both clear skies (maximum three-quarters cloud cover with the position of the sun always visible) and overcast (more than seven-eighths cloud cover with the sun position always obscured). Further, we ran the experiments under two different magnetic conditions: (i) control, tests in the local unmanipulated geomagnetic field; and (ii) deflected, experiments in which magnetic north was shifted 90° counterclockwise (i.e. geographic 249°). Orientation tests were performed in flat and open areas without any visual landmarks in the vicinity. The funnels were placed in sand containers, either directly on the ground (control birds) or in the centre of

Fig. 1. (A) The location of the study site in southwest Iceland (Sandgerdi) is indicated by a star. The black dot on the east coast of Greenland depicts one recovery during the breeding period of a sanderling ringed in Iceland at the spring stopover. (B) Flight directions of sanderling flocks departing from southwest Iceland in May–June 1988–1990 as measured by visual observations. The departure direction of each flock is indicated by a dot, to the nearest 10° . The mean vector and the angular deviation (dotted lines) were calculated to the nearest degree (redrawn after Gudmundsson and Lindström, 1992). (C) Circular diagram showing the declination between geomagnetic north (mN) and geographic north (gN) at the study site. In addition, the position of magnetic north during experimental deflections of the magnetic field performed in cage tests (mN -90°) is illustrated.



the cubic magnetic coils standing on levelled wooden platforms approximately 15 cm above ground (experimental birds). Although the experimental birds could see the coils during tests, the cubic and thus symmetrical shape of the coils should have precluded any biasing influence on the directional behaviour of the deflected group. All funnels were situated at least 3 m apart. Experiments commenced between 19:10 h and 01:00 h local Icelandic time (UTC) and lasted for 1 h.

Data and statistical analyses

Individual sanderlings were tested only once. A preliminary quantification of the amount of migratory activity was made by counting the number of scratches left in the pigment of the Tipp-Ex papers in the funnels up to a minimum of 50, which was set as the limit for inclusion of individual tests. We also excluded bird-hours that failed to show a reasonably well-defined orientation. To do this, we subdivided each Tipp-Ex paper into 12 sectors and examined the spread of scratches. When scratchmarks covered more than half (more than six sectors) of the paper and no obvious modal direction was discernible (see below), the test-hour was considered disoriented and excluded from further analysis. Finally, since axial distributions (i.e. when the two modes were of equal strength) do not give unambiguous information concerning the directional choices of individual birds, we excluded individuals showing bimodal orientation (see Table 1).

The modal direction of the activity of each bird was

evaluated according to the method described by Cherry and Able (1986). This method was used because of the difficulty in quantifying the number of scratches in sectors where the pigment had been completely removed. Modal directions were then pooled to obtain sample mean vectors according to standard procedures (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). Differences in mean direction between samples (indicated by $F_{1,d,t}$) were examined using the one-way classification test, and differences in the concentrations around the mean angle (indicated by t) were compared between test categories using the test for the homogeneity of concentration parameters (Mardia, 1972). If one or both the samples was randomly distributed or bimodal, Watson's U^2 -test (indicated by U^2) was used (Batschelet, 1981).

Timing of tests and the basis for grouping data in relation to tide

Sanderling foraging pattern on the seashore is closely linked to the tidal cycle (Fig. 2). They usually forage at the water's edge or in areas washed by waves on sandy shores and on mudflats that are exposed during low water. Foraging near the water's edge is more intensive during a retreating rather than a rising tide (G. A. Gudmundsson and R. Sandberg, personal

Table 1. Number of tests used for analysis and numbers of tests excluded on the basis of inactivity (<50 scratches per hour), disorientation and bimodality relative to the total number of birds tested

Experimental condition		Analysis	Inactivity	Disorientation*	Bimodality*	Total
Clear sky	Control	30	3	11	4	48
	Deflected	27	2	9	8	46
	Sum	57	5	20	12	94
Overcast	Control	54	15	13	19	101
	Deflected	48	10	15	5	78
	Sum	102	25	28	24	179

*See Materials and methods.

χ^2 -tests did not reveal any statistically significant differences between experimental categories under either clear or overcast skies. The only significant difference was between the total number of inactive tests under clear skies and those under overcast conditions (number of inactive tests: five *versus* 25, $\chi^2=4.7$, $P<0.05$).

observation). Roosting begins soon after low tide and finishes soon after high tide. Therefore, unlike many other shorebirds, e.g. knot (*Calidris canutus*; Alerstam et al., 1990), sanderling roosting is neither correlated with tidal level nor is it symmetrical around high water.

Departures of shorebirds on long-distance migration from stopover sites have a tendency to take place in the late afternoon and evening close to sunset (Gudmundsson, 1994), although correlation with tidal stage has been found within that time frame (Alerstam et al., 1990). Observations of departing sanderling flocks from southwest Iceland (Gudmundsson and Lindström, 1992) show a similar pattern, with half the observed departures taking place between 20:00 and 24:00 h (constituting only 16% of the total observation time). Furthermore, a great majority (77%) departed at low water ± 3 h, indicating that, when sanderlings are ready to depart (i.e. refuelling has been completed and the weather is suitable), they do so during a tidal window centred around low water. This suggests that, when foraging activity decreases at low water, the birds either begin to roost or decide to depart (Fig. 2).

Results

Orientation under clear skies

Sanderlings tested in the local geomagnetic field (controls)

under clear skies selected a mean direction towards geographic north (see Fig. 3, top left). This control direction was closely similar to information from the only available ringing recovery and data from visual observations of departing sanderling flocks (Gudmundsson and Lindström, 1992; see Fig. 1) and significantly different from the mean sun azimuth (sun position outside 95% confidence interval $\pm 24^\circ$). When magnetic north was experimentally shifted 90° counterclockwise from its normal position (deflected), the sanderlings responded with a significant counterclockwise shift in mean direction of 73° ($F_{1,55}=8.4$, $P<0.01$; see Fig. 3, top right). Although not significant, there was a considerable difference in directional scatter between controls ($r=0.59$) and deflected ($r=0.33$) birds, with the latter group being on the verge of randomness.

However, if we take into account the tidal window during which sanderlings normally depart (Fig. 2), then the concentration of preferred directions increases for both categories (Fig. 3, middle diagrams). The largest increase occurred for the deflected group (r increased from 0.33 to 0.48) since one-third of the individuals in the total sample were tested outside the tidal window given in Fig. 2. In addition to making the scatter in the control and deflected categories more equal, the counterclockwise shift increased from 73 to 82° ($F_{1,42}=12.1$, $P<0.005$), which is close to the expected 90°

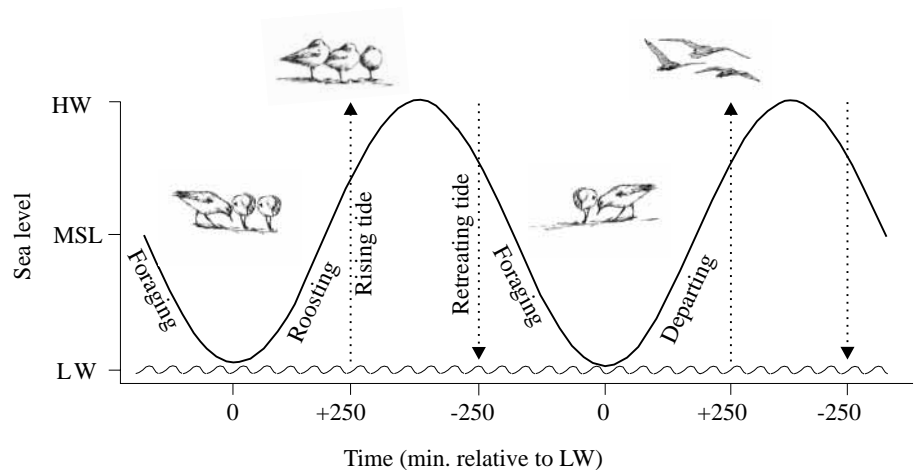
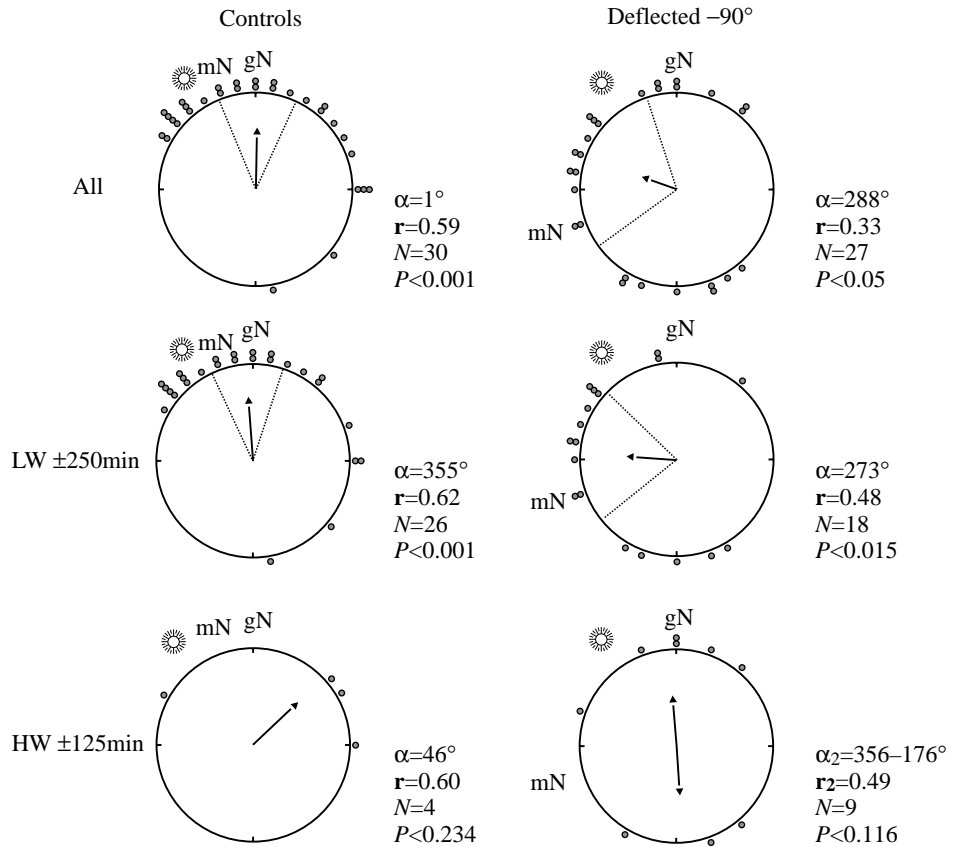


Fig. 2. A schematic illustration of the activity pattern of sanderlings in relation to the tidal cycle. As the season progresses, the sanderlings depart (see the text for further information on departure behaviour) instead of roosting as the tide rises. LW, low water; HW, high water; MSL, mean sea level. The tidal window ($LW \pm 250$ min) used for grouping the data is indicated.

Fig. 3. Orientation under clear skies of sanderlings (*Calidris alba*) as registered by funnel experiments during the spring migration passage in southwest Iceland. The left-hand column shows the outcome of control experiments (unmanipulated local geomagnetic field), and the right-hand column illustrates the orientation behaviour of the birds when exposed to a magnetic field shifted 90° counterclockwise. Diagrams in the top row show the summary results for the two test categories; the middle and bottom rows display the results when subdivided into tests performed within the tidal window (LW±250 min) and outside the tidal window (HW±125 min), respectively (see Fig. 2). Each symbol outside the periphery of the circles represents the modal direction for one individual. The mean position of the sun is also indicated outside each circular diagram. Similarly, the direction towards magnetic north (mN) is shown in relation to geographic north (gN). The mean direction (α) of each sample is shown by an arrow or, in the case where a mean axis of orientation provided a better fit to the data, a double-ended arrow (α_2). 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). Confidence intervals (95 %) are shown as dotted lines around the mean vector or axis (unimodal distributions, see Batschelet, 1981; bimodal distributions, see Prentice, 1984). Significance levels (P) were calculated according to the Rayleigh test (Batschelet, 1981); N is the number of tests. LW, low water; HW, high water



difference. Furthermore, the mean direction of the deflected group became significantly different from the mean sun azimuth (95 % confidence interval $\pm 40^\circ$).

The directional behaviour of sanderlings tested outside the tidal window (prone to either roosting or foraging) is shown in the bottom diagrams in Fig. 3.

Orientation under overcast

Control birds tested under natural overcast conditions showed a bimodal distribution of preferred headings, coinciding approximately with a magnetic north-south axis (321–141° or -18° away from the magnetic axis; Fig. 4A).

The orientation of controls under overcast was significantly different from their directional behaviour under clear skies ($U^2=0.429$, $P<0.001$). Sanderlings tested in a deflected magnetic field displayed a non-significant axis (222–42°) shifted -99° from the direction of controls towards the expected direction (Fig. 4B). However, the experimental category was too scattered to allow any inferences, and there was no statistical difference in orientation behaviour between the two samples (control *versus* deflected, $U^2=0.164$, $P>0.05$). Unfortunately, it was not possible to analyse the orientation behaviour of sanderlings in relation to the prevailing tidal regime (see above) since too few individuals (only two control

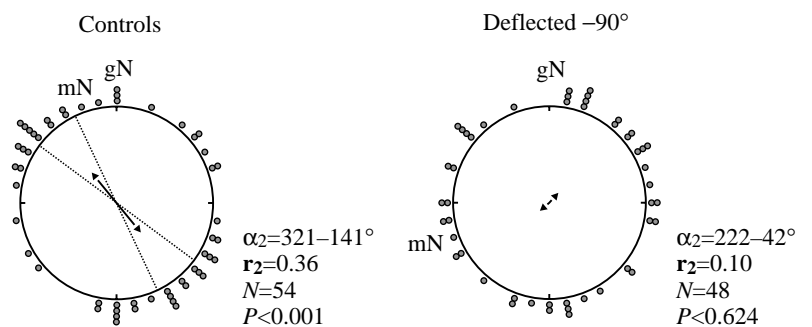


Fig. 4. Orientation cage experiments under overcast with sanderlings (*Calidris alba*) on their spring migration through southwest Iceland. See legend to Fig. 3 for further details.

and five experimental birds) were tested outside the tidal window shown in Fig. 2.

We investigated whether there were any differences in the proportions of inactivity, disorientation or bimodality between tests under clear and overcast skies, respectively, and found that sanderlings were significantly more likely to become inactive under overcast than under clear skies ($\chi^2=4.7$, $P<0.05$, see Table 1).

Discussion

Hitherto, all investigations concerning the capacity to use the geomagnetic field as a directional source for avian migratory orientation have focused on passerine birds as test subjects. Our results clearly demonstrate that sanderlings consistently exhibit measurable, oriented activity in Emlen funnels. Under clear sky control conditions, the directional behaviour of the birds is in excellent agreement with earlier observational data on departure directions from Iceland (Gudmundsson and Lindström, 1992) and with the available ringing recovery data. Furthermore, the evidence presented here shows, for the first time, that a wader species is capable of detecting and using the geomagnetic field for orientation. The experiments indicate that sanderlings use primarily geomagnetic cues for their migratory orientation under clear sky conditions. However, contrary to our expectations, similar clearcut evidence could not be obtained under overcast skies.

The location of our study site is of particular interest since it is situated at a high geographic and geomagnetic latitude close to the Arctic circle. Quite possibly, the most intriguing challenge to the orientation system of migratory birds is illustrated by species that migrate across high latitudes because they will have to face an extreme orientation cue environment. For example, the steep inclination of the geomagnetic field may make the magnetic inclination compass unreliable or even unusable, the use of the sun compass involves problems with time compensation during rapid passage through the compressed longitudes and, finally, the stars are not accessible when spring-migrating birds enter the polar area (continuous daylight from the end of May onwards) and will not become visible until around mid-August (Alerstam, 1990; Alerstam et al., 1990; Sandberg et al., 1991; Gudmundsson and Alerstam, 1998). There are several possible ways for the birds to overcome these problems. They may rely primarily on solar cues and, in the case of sanderlings departing from Iceland towards breeding areas in northeast Greenland, time compensatory problems might not be an issue since they are expected to travel in a geographic northerly direction (Fig. 1). Their other option would be to rely primarily on the magnetic compass. It has been suggested that, by following magnetic loxodrome courses (tracks with a constant magnetic compass course) in the sectors between 60°E and 60°W (which includes our study site and expected destinations) and between 130°W and 130°E, the birds reduce their flight distance (Alerstam and Hedenström, 1998).

Although our data indicate that geomagnetic cues are of

primary importance for the orientation of sanderlings under clear sky conditions, control experiments under natural overcast seem to suggest that access to celestial cues is of importance for achieving a correct migratory orientation. The axial behaviour of control birds under overcast skies is puzzling since we would have expected that, in the absence of visual directional information, the birds should have been able to make use of the available geomagnetic information. Instead, approximately half the birds tested opted for headings coinciding with magnetic south. The underlying reason for this behaviour can only be speculated upon. One possibility is that migratory birds, including sanderlings, are less motivated to depart from stopover sites under overcast skies and either become inactive or display reverse orientation (Richardson, 1982; Sandberg et al., 1988; Piersma et al., 1990; Sandberg, 1994; Åkesson et al., 1996). For example, Piersma et al. (1990) noted that, during 277 autumn departures of waders from The Netherlands, the sun was always visible and no flocks were observed leaving under overcast. The fact that our sanderlings were significantly more likely to become inactive under overcast skies than under clear sky tests lends some support to this explanation.

Another possibility is that the steep inclination of the geomagnetic field (+75° at our study site) might make magnetic directional information ambiguous or unreliable (Wiltschko et al., 1998). Findings indicating the necessity of having access to both celestial and geomagnetic cues for appropriate unimodal orientation involve, almost exclusively, studies on hand-raised birds. To our knowledge, the only studies showing bimodal magnetic orientation in wild-caught birds were performed with Savannah sparrows (*Passerculus sandwichensis*) during the autumn migration period (Bingman, 1981; Able and Able, 1995). However, during spring tests with Savannah sparrows under the same conditions, the orientation became unimodal (Able and Able, 1996). In conclusion, we find that the available data are too scant to distinguish between these two rather speculative explanations, and future research is clearly needed to resolve this issue.

Even more perplexing is the behaviour of sanderlings tested under overcast skies in experimentally deflected magnetic fields. Despite the weak tendency for an axial response more-or-less in the expected direction, the results seem more to reflect utter confusion than anything else. To become confused by a shifted magnetic field in the absence of celestial cues, the birds would have to be able to measure the shifted position of magnetic north in relation to some other external reference. Without resorting to speculations about as yet undiscovered directional cues, we have to admit that we cannot find any plausible explanation for the behaviour displayed by the experimental group under overcast conditions.

In conclusion, shorebirds seem to be well suited for experimental investigations of their orientation capacity and, taken together with the extraordinary features of their well-documented migratory flights and life history characteristics, this makes them highly interesting as test subjects in future carefully controlled cage experiments.

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