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Orientation Cage and Release Experiments with Migratory Wheatears (*Oenanthe oenanthe*) in Scandinavia and Greenland: The Importance of Visual Cues

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Abstract

Migratory orientation of Scandinavian and Greenland wheatears was recorded during the autumn migration periods of 1988 and 1989. Orientation cage tests were conducted under clear sunset skies, to investigate the importance of different visible sky sections on orientation performance. In addition, wheatears were released under clear starry skies and under total overcast to examine the orientation of free-flying birds. The following results were obtained:

(1) Wheatears tested with a restricted visible sky section (90° centered around zenith) in orientation cages, showed a mean orientation towards geographic W/geomagnetic NW (Greenland) and towards geographic and magnetic WNW-NW (Sweden). These mean directions are clearly inconsistent with the expected autumn migration directions, SW-SSW in Scandinavia and SE in Greenland, as revealed by ringing recoveries for the two populations.

(2) When the birds were allowed a much more extensive view of the sky, almost down to the horizon (above 10° elevation), Scandinavian wheatears chose headings in agreement with ringing data. Greenland birds were not significantly oriented.

(3) Release experiments under clear starry skies resulted in mean vanishing directions in good agreement with ringing data from both sites. Greenland wheatears released under total overcast showed a similar orientation as under clear skies, indicating that a view of the stars may not be of crucial importance for selecting a seasonally accurate migratory direction.

The results suggest that an unobstructed view of the sky, including visual cues low over the horizon, is important, possibly in combination with geomagnetic cues, for the orientation of migratory naive wheatears. Furthermore, the birds showed remarkably similar orientation responses in Greenland and Scandinavia, respectively, indicating that they use basically the same orientation system, despite considerable differences in visual and geomagnetic orientation premises at the two different geographic and magnetic latitudes.

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Introduction

Migratory birds are capable of deriving directional information from a number of different environmental sources. In particular, nocturnally migrating birds may use the sunset azimuth, skylight polarization pattern, the stars and geomagnetic cues to determine a migratory direction (ABLE 1980, 1989; WILTSCHKO 1983; BAKER 1984; MOORE 1987). Recent orientation cage experiments have shown that a view of the setting sun is important for the orientation of savannah sparrows (*Passerculus sandwichensis*) (MOORE 1978, 1980). The same is true for two other short- to medium-distance migrants, the white-throated sparrow (*Zonotrichia albicollis*) and the robin (*Erithacus rubecula*), both of which seem to depend on an unobstructed view of the sunset sky for their orientation (BINGMAN & ABLE 1979; KATZ 1985; SANDBERG, in press). Furthermore, MOORE (1982) was able to shift the orientation of Savannah sparrows by manipulating the direction towards sunset with mirrors. However, since it has been demonstrated that migratory birds, e.g. white-throated sparrow, several Parulinae warblers and blackcaps (*Sylvia atricapilla*), also respond to experimental changes of polarized light (ABLE 1982; MOORE 1986; MOORE & PHILLIPS 1988; HELBIG & WILTSCHKO 1989), the relative importance of polarization patterns and the sunset position has not been assessed conclusively.

Cage studies of migratory orientation offer convincing evidence that nocturnally migrating birds also possess a magnetic compass (WILTSCHKO & WILTSCHKO 1988). Relatively few experiments have been performed to evaluate the priorities of geomagnetic and visual information during the twilight period. By altering the sunset position with mirrors 90° clockwise and simultaneously changing the direction towards geomagnetic north 90° counterclockwise, MOORE (1985) showed that savannah sparrows rely primarily on visual cues at sunset, in spite of the fact that these birds have a magnetic compass (BINGMAN 1981). Robins that were tested in deflected magnetic fields during twilight, displayed an axial response which confirmed the use of magnetic cues, but suggested that additional (probably visual) cues are required to establish magnetic polarity (SANDBERG et al. 1988b). Finally, BINGMAN & WILTSCHKO (1988) found that dunnocks (*Prunella modularis*) appear to use the Earth's magnetic field as a primary directional reference at sunset.

Experiments with wheatears (*Oenanthe oenanthe*) in Sweden and Greenland during the autumn migration period, demonstrated that they have the ability to use geomagnetic cues for orientation purposes (SANDBERG et al., in press). Without access to visual cues (simulated total overcast), the birds changed their orientation in close accordance with experimental shifts of the magnetic field direction. However, when tested under clear sunset skies the wheatears were less influenced by geomagnetic manipulations, thus pointing to an importance of celestial cues during twilight. In control experiments, under clear as well as overcast skies, both Scandinavian and Greenland birds selected mean directions towards magnetic NW which is clearly different from the expected autumn migration directions.

These experiments with wheatears were all conducted using screens around the orientation cages. Hence, the sky section that was visible to the test birds was

reduced to about 90° around zenith. To investigate if an unobstructed view of visual cues close to the horizon is important for selecting a seasonally appropriate migratory direction, wheatears were tested in orientation cages with access to a visible sky section of either 90° or 160°. Experiments were performed at Ottenby in South Sweden, during the autumn migration period in 1989. In addition, to examine the orientation behaviour at high geographic and magnetic latitudes where the premises for using solar, stellar and geomagnetic cues are considerably different (ALERSTAM et al. 1990), a parallel test series was run on the island of Disko at the west coast of Greenland, using the same experimental design. Finally, to study the orientation performance of free-flying wheatears under clear starry skies and under total overcast, respectively, release experiments were conducted in both Sweden and Greenland.

Materials and Methods

1. Test Species

The wheatear, a nocturnal migrant, has a spectacularly wide geographical distribution, with breeding populations ranging from Northeast Canada, Greenland, Iceland, and continuing across Europe and Asia to Alaska (CRAMP 1988). All these birds winter in Africa, south of the Sahara, and perform some of the most extraordinary migratory journeys known, e.g. from Alaska to East Africa, and from Greenland by way of southwestern Europe to West Africa (SALOMONSEN 1967; MOREAU 1972; CONDER 1989). Two different populations were studied during autumn migration in Sweden (*O. o. oenanthe*) and Greenland (*O. o. leucorhoa*), respectively.

Test birds used in the orientation cage study at Ottenby in Sweden (56° 12'N, 16° 24'E) were captured either as newly fledged, or as passage migrants. Following capture, the wheatears were transported to a test site about 3 km north of the bird observatory. The fledglings were held in captivity until the autumn migration period commenced. All birds were housed in individual cages made of nonmagnetic materials, and were exposed to the local geomagnetic field and the natural photoperiod.

Greenland wheatears, used both in orientation cage studies and in release experiments, were taken from nests located in the surroundings of the Arctic Field Station in Godhavn (69° 18'N, 53° 40'W), on the island of Disko at the west coast of Greenland. Nestlings from the same brood were held in captivity together with the parent female or male, who fed their young until they reached an age of about 20–25 days. At that time, the birds were transferred to individual cages in a room with windows facing south, and were exposed to the local geomagnetic field and the natural photoperiod. Supplemental birds were captured in mist nets after the onset of migration in the vicinity of the field station.

Finally, the birds used in the Swedish release experiments were all captured as passage migrants at Falsterbo Bird Observatory (55° 23'N, 13° 25'E) and transported by car to the test site (Stensoffa Ecological Field Station) approximately 55 km to the northeast of Falsterbo.

The housing and maintenance of the experimental birds as well as the test sites have been described in more detail by SANDBERG et al. (1988a, in press).

2. Experimental Procedure

(A) Orientation cage experiments. All cage experiments were carried out using either modified Emlen-funnels (Greenland) with automatic registration of migratory activity in 8 sectors (SANDBERG et al. 1988a), or plastic funnels (Sweden) of the same size but with typewriter correction paper as the recording medium (RABØL 1979; BECK & WILTSCHKO 1981).

The wheatears were tested under clear skies (median cloud cover: 1/8, range: 0/8–3/8), and in the local geomagnetic field. Experimental birds were placed inside the cages and carried to the test area about 30 min before local sunset (Greenland). Cages with typewriter correction paper were carried to

the test area about 10 min before the onset of experiments with a piece of cloth covering the cage (Sweden). Registration of migratory restlessness started 10 min after the sun had set and lasted for 1 h (i.e. until the first stars became visible). The only difference between the experiments in Greenland and Sweden was that the Greenland birds could observe the sky during the sunset period before registration, while this was not possible for the Swedish birds tested in cages with typewriter correction paper.

Test conditions: (1) With screens — orientation cages were placed inside large plastic tubes that restricted the visible sky section to approximately 90° above (SANDBERG et al. 1988a). This setup prevented the birds from seeing nearby landmarks and the lower parts (below 45° elevation) of the sunset sky. (2) Without screens — orientation cages were put on top of wooden boxes (0.5–1 m above ground level), giving the birds an almost unrestricted view of the twilight sky (about 160° above). Although the disc of the setting sun was not visible to the birds, they were able to see the brightest part of the sky low over the horizon. The Swedish test series, conducted at Ottenby, was performed between 5 Sep. and 6 Oct. 1989, using a total of 24 wheatears. The Greenland experiments started on 12 Aug. and lasted until 9 Sep. 1989 (condition 1: 35 individuals, condition 2: 15 individuals).

(B) Release experiments. To study the orientation performance under as natural conditions as possible, a technique similar to the method described by ABLE & TERRIL (1987) was used. A small chemiluminescent plastic container (Cyalume Lightstick, 2.9×24 mm, 0.15 g, green 95281-17, American Cyanamid Co.) is attached to the two outermost rectrices on one side of the tail with transparent adhesive tape. Before fastening, the stick is flexed in order to break a small enclosed glass container, allowing two chemical components to mix. The subsequent chemical reaction produces a clearly visible green light. Under weather circumstances with good visibility, we have estimated maximum tracking distances between 700–1000 m. When the tape gets damp the light capsule will fall off the bird.

Experimental birds are tossed into the air much in the same way as homing pigeons and then followed using 10×40 binoculars until they have vanished from sight. This method permits observations of flight behaviour and recordings of vanishing times and bearings. It is usually easy to assess whether the birds are motivated to migrate or not because they typically either ascend while circling and subsequently take off on a straight course, or land almost immediately.

Release experiments were conducted under either clear starry skies (median cloud cover: 2/8, range: 0/8–4/8), or under total overcast (Greenland only), with no or light winds. These tests were run after the conclusion of orientation cage experiments for each individual, when the birds would have been released anyway. The Swedish releases were performed from 13 Sep. until 2 Oct. 1988 (4 nights). The corresponding releases in Greenland were conducted between 1 and 13 Sep. 1989 (7 nights). The birds were released singly and vanishing directions were recorded to the nearest 1° with a compass, and vanishing intervals were registered by a stop watch.

Prior to all tests, the wheatears were weighed to the nearest 0.1 g with a Pesola spring balance and fat deposits were estimated visually on the birds' bellies according to a 7-class scale (PETTERSSON & HASSELQUIST 1985). Winglengths were measured on fully grown birds to the nearest 1 mm (maximum winglength, see SVENSSON 1984).

3. Data Analysis and Statistical Evaluation

Individual wheatears were tested only once under each of the two orientation cage conditions described above. Each bird's migratory activity was quantified (40 counter registrations/scratches minimum), and a mean heading was calculated by vector addition. Bird-h that failed to show a reasonably well-defined orientation — the limit was arbitrarily set to $m^2 < 3.0$ (n = number of counts, r = vector length) — were excluded. 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 limit was not used as a measure of statistical significance, but simply as a yardstick for exclusion of bird-h that yielded unreliable estimates of orientation. This procedure led to exclusion of 7 test-h (2 inactive and 5 with a wide scatter, Greenland) and 2 test-h (both inactive, Sweden), respectively. Mean headings were pooled for each experimental condition to obtain sample mean vectors, according to standard procedures given in BATSCHELET (1981). Vanishing bearings of released wheatears were treated in the same way and a mean vector was calculated for each sample.

To obtain the best possible description of the angular distributions, we compared the average unimodal vector length (r) with the corresponding mean vector length resulting from doubling the angles (r_2), and chose the largest of the two. Differences in mean directions between experimental categories were examined by using the 'one-way classification test' (MARDIA 1972), or Kuiper's test in case one of the involved angular distributions was nonsignificant according to the Rayleigh test (BATSCHELET 1981). Orientation scatter was compared among samples with the 'test for the homogeneity of concentration parameters' described by MARDIA (1972).

Results

1. Orientation Cage Experiments

Scandinavian wheatears deprived of a view of the sunset sky below 45° elevation (condition 1), showed a highly concentrated mean orientation close to the average sunset azimuth (Fig. 1). This mean direction is similar to the corresponding results obtained at Ottenby during autumn migration in 1988 ($\alpha = 329^\circ$, $r = 0.62$, $n = 13$, $p < 0.01$, mean sunset position = 298° ; SANDBERG et al., in press). Hence, it can be concluded that in spite of the difference in registration techniques (1988: automatic counter registration vs. 1989: typewriter correction paper), the seasonally inappropriate WNW—NW mean direction remained unchanged. In addition, the 1989 series of orientation experiments was performed

CLEAR SKY

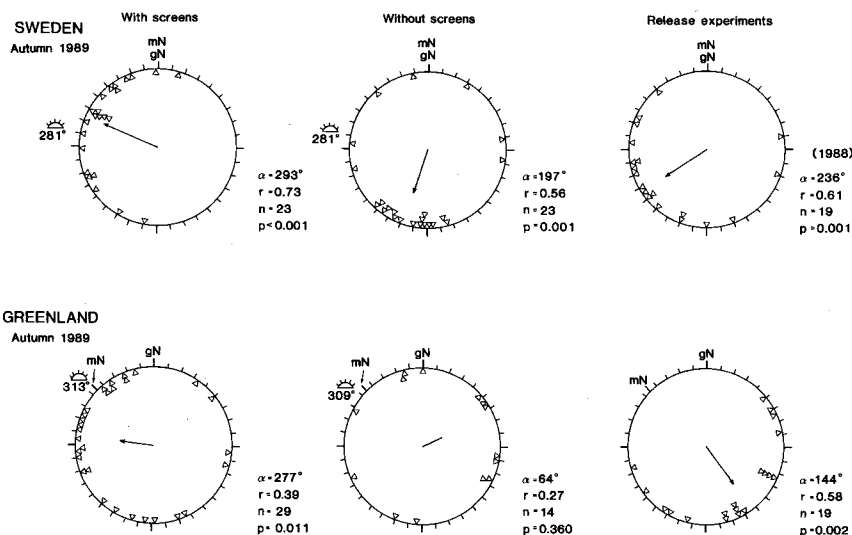


Fig. 1: Orientation of wheatears under clear sunset skies, during autumn migration. Top: Scandinavian wheatears; bottom: Greenland birds. Left: orientation cage tests with screens (visible sky sector reduced to approx. 90°); middle: cage tests without screens (visible sky section about 160°); right: free-flying wheatears under clear starry skies. Average position of the setting sun, in the middle of the test hour, is indicated outside the diagrams. The direction towards geomagnetic north (mN) is marked in relation to geographic north (gN). Each triangle represents a mean heading of one individual. Arrow: mean vector (α), vector length (r) is proportional to the radius of the circle = 1. p according to the Rayleigh test (BATSCHELET 1981)

somewhat later during the autumn migration period than the 1988 tests (difference in mean sunset position = -17°), and the wheatears chose on average slightly more westerly headings (-36° , comp. Fig. 1 and above).

When the Scandinavian wheatears were afforded a much more extensive view of the sunset sky (condition 2), they showed a significantly different mean orientation towards SSW ($p < 0.001$). This mean direction is also clearly distinct from the average sunset azimuth ($p < 0.01$), and in good agreement with the expected autumn migration course for Swedish wheatears, as revealed by ringing recoveries (see below). Hence, the amount of visible sky section had a profound effect on the orientation of the wheatears.

Greenland wheatears tested under a visually restricted sky sector preferred a mean direction towards geographic W (corresponding to geomagnetic NW), i.e. they oriented in a seasonally incorrect autumn migration direction that was statistically inseparable from the average position of the setting sun ($p > 0.05$).

In contrast, when the Greenland birds had access to an almost unrestricted view of the sunset sky, they changed their preferred headings towards more easterly directions (Fig. 1). Unfortunately, the sample size was small and failed to reveal a significant orientation. Comparing the results of screened and unscreened tests for individuals that were exposed to both experimental conditions discloses a significant difference in circular distributions ($p < 0.05$, Kuiper's test). However, Kuiper's test (BATSCHLET 1981) does not specify if the difference is in the mean direction, or in the angular variance, but there was no statistically significant difference in orientation scatter between the two samples.

2. Release Experiments

Of the 21 wheatears that were released in Sweden, 19 (90 %) gained considerable height and remained flying at high altitude until they vanished from view. As shown in Fig. 1, the Scandinavian wheatears showed a well-defined mean departure direction towards southwest as expected on the basis of ringing recoveries (cf. below). The duration of individual vanishing intervals ranged from 49 to 247 s (\bar{X} : 99 s, $SD \pm 49$ s). Assuming an approximate airspeed of 10 m/s leads to average tracking distances of up to 1 km. Individual behaviour of the released birds varied from initial circling while gaining height (2–3 full circles, long vanishing intervals) before taking off on a straight course, to a rapid climb along a wide arc which was succeeded by straight and level flight (short vanishing intervals).

In the Greenland experiments, 39 wheatears were released under clear starry skies and 19 (49 %) were classified as successfully taking off on migratory flights. The resulting mean direction towards southeast (Fig. 1) is in good agreement with ringing data (see below). Flight behaviour and vanishing intervals were closely similar to the Swedish releases (mean vanishing interval: 76 s, $SD \pm 38$ s, range: 35–203 s). Of the total sample ($n = 39$), 23 were caught as passage migrants and 16 were raised indoors from an age of about 10 days, respectively. The proportion of successful releases for the former category was 61 % (14/23) whereas only 31 % (5/16) of the birds that lacked previous flight experience took off and

vanished without landing in the vicinity of the release site. This relatively large difference in success rate was, however, not significant ($\chi^2 = 2.2$, $p > 0.1$). There was a tendency for lower success rate in releases of Greenland passage migrants as compared to Scandinavian birds (61 % vs. 90 %, $\chi^2 = 3.7$, $p \leq 0.06$).

The success rate of releases conducted under total overcast in Greenland was 69 % (11 out of 16 individuals). Despite a small sample size, the birds departed in an appropriate mean direction towards ESE (Fig. 2). Released wheatears tended to circle more under overcast skies before they determined a heading, and as a consequence, vanishing times were on average slightly longer (\bar{X} : 98 s, SD \pm 43 s, range: 48—204 s).

TOTAL OVERCAST

Release experiment

GREENLAND
Autumn 1989

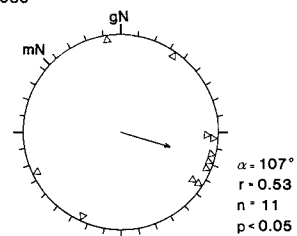


Fig. 2: Migratory orientation of Greenland wheatears released under total overcast. See Fig. 1 for further details

There are two possible confounding variables that could have affected the directional choices of the released wheatears, namely the influence of wind and topographical features. Since all releases were conducted on evenings with no or light winds (≤ 2 m/s), the possible biasing influence of this factor can essentially be ruled out. At the Swedish release site there is an extensive woodland in the east quadrant and a more restricted grove to the west whereas the north and south quadrants are open areas. As the Scandinavian wheatears selected headings towards SW, they passed over the southern portion of the grove at high altitude, i.e. there is no reason to suspect a biasing influence by this variable. The same is true for the Greenland site where high ground (mountain ridges) surrounded the release point in the sector from about WNW over N to ENE. The release site was close to the open sea, with a shoreline running approximately W—E only a few hundred meters south of the test site. On a small peninsula to the SW, the village of Godhavn is situated. If the Greenland birds were attracted to prominent topographical features like the mountain ridges, and tried to avoid the open sea, we would have expected more headings in the northern quadrant or along the coastline towards W or E. Similarly, a possible biasing influence of horizon glow from Godhavn should have resulted in a more pronounced occurrence of SW headings if the wheatears were attracted towards this light source (there was no artificial horizon glow in the vicinity of the Swedish release site).

3. Evidence from Ringing Recoveries

Recoveries of Swedish and Greenland wheatears, ringed either as nestlings during the summer or at the beginning of autumn migration, and subsequently recovered during the same autumn migration period, are shown in Fig. 3. The inset circular diagrams reveal highly clustered angular distributions towards SW (from Sweden) and SE (from Greenland), respectively.

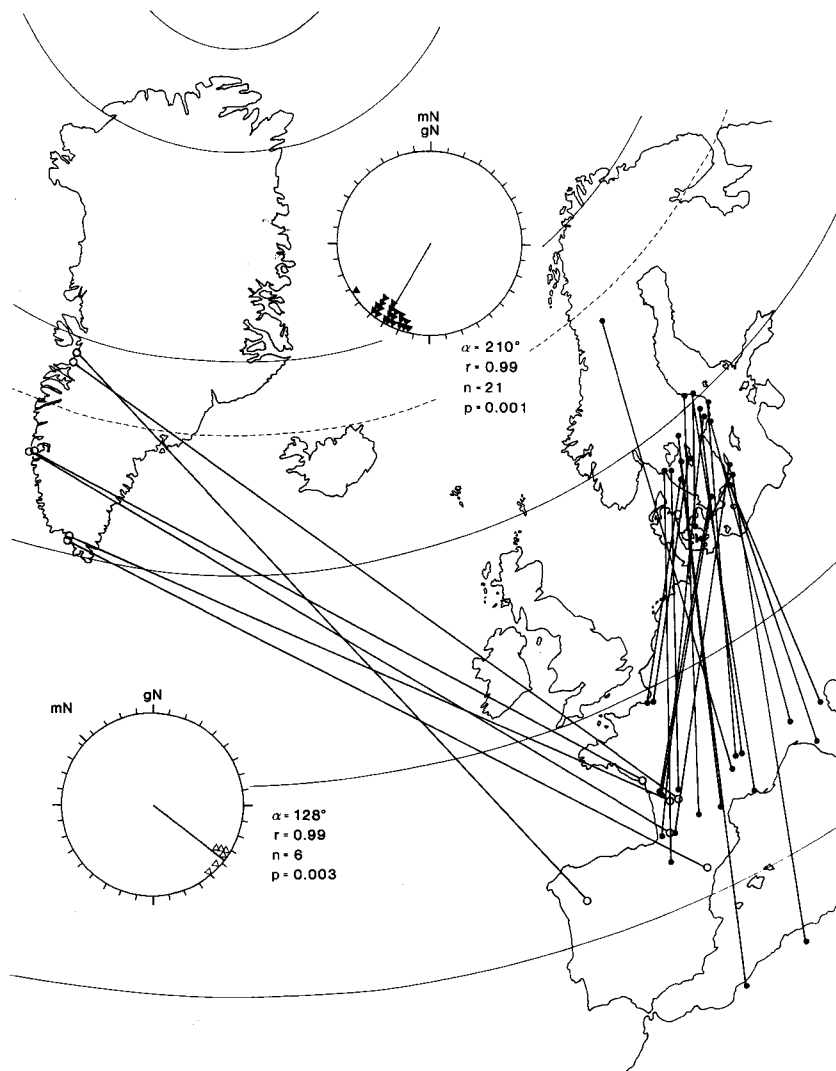


Fig. 3: Ringing recoveries during autumn migration (from end of Aug. until Nov.) of wheatears ringed previously during summer or the beginning of autumn migration in Sweden (closed symbols) and Greenland (open symbols). Compass courses from ringing sites to recovery positions were calculated, and mean vectors of these bearings are presented in the circular diagrams. Ringing data for Greenlandic wheatears were communicated by the Zoological Museum in Copenhagen through K. KAMPP, and the corresponding data from Sweden were supplied by the Museum of Natural History in Stockholm through R. STAAV

The mean rhumbline distance between ringing and recovery sites for Swedish wheatears is 1760 km, and the corresponding mean distance for Greenland birds is 3850 km. Consequently, the wheatears from Greenland depart on a migratory leg that is more than twice as long as the corresponding distance for the Swedish birds. In addition, the Greenland population embark on a migratory journey that mainly consists of a flight across the Atlantic (at least 3400 km, from the southernmost point of Greenland). This is nicely reflected in the amount of fuel reserves stored before taking off on migration (Fig. 4). The relative increase in body mass of Greenland wheatears was almost twice as high as that of Scandinavian birds ($p < 0.001$, Table 1). Actually, if we compare the increase in body mass of the 8 heaviest individuals (upper quartile) between birds tested in Sweden and Greenland, respectively, the latter category increased their body mass approximately 2.5 times more from the nonmigration phase than did the Scandinavian birds (mean increase = 24.2 g and 9.8 g, Fig. 4).

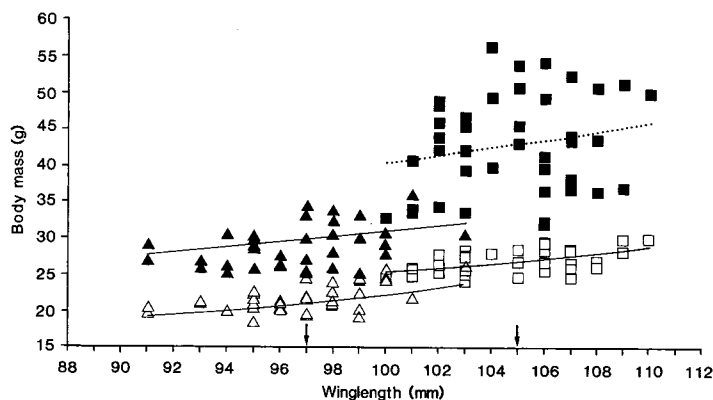


Fig. 4: Comparison of body mass vs. winglength for Scandinavian and Greenland wheatears during the nonmigratory and migratory phase, respectively. Nonmigratory phase — open triangles: Scandinavian birds (regression line: $Y = 0.007 * X^{1.74}$, $n = 36$, $P < 0.001$), open squares: Greenland birds (regression line: $Y = 0.100 * X^{1.19}$, $n = 38$, $p < 0.005$). Migratory phase — closed triangles: body mass of Scandinavian wheatears (regression line: $Y = 0.122 * X^{1.18}$, $n = 39$, $p < 0.05$), closed squares: corresponding data for Greenland birds (regression line: $Y = 0.100 * X^{1.31}$, $n = 42$, $p = 0.2$). Median winglengths for the two categories are indicated by arrows

Discussion

We have recently demonstrated that migratory wheatears possess a magnetic compass (SANDBERG et al., in press). Orientation cage tests under simulated total overcast revealed that the birds are able to use the geomagnetic field as a directional reference, even at the high magnetic latitudes in West Greenland. However, the wheatears were distinctly less influenced by experimental manipulations of the geomagnetic field direction under clear sunset skies. Furthermore, there was a consistent attraction towards magnetic northwesterly mean directions, under both clear and overcast skies, that is clearly different from the expected autumn migration directions based on ringing recoveries (Fig. 3).

Table 1: Comparison of body reserves of Scandinavian and Greenland wheatears during the nonmigratory and migratory phase. Estimate of stored migratory fuel supplies according to PETRIE (1983), i.e. body mass was divided with winglength³ to compensate for differences in body size between the two populations (Fig. 4). Nonmigratory body mass was measured during Jul. and the beginning of Aug. and was restricted to individuals with a visually estimated fat load of ≤ 2 (PETTERSSON & HASSELQUIST 1985), and the corresponding data on migratory body mass refer to wheatears with visual fat deposits of ≥ 5 , attaining their maximum body mass mainly during Sep. Statistical evaluations by t-test

	Sweden	Greenland	p
A: Nonmigratory phase			
Body mass (g)/winglength ³ (mm) ($\times 10^{-6}$, \pm SD, n = 38, 36)	24.1 \pm 1.8	23.5 \pm 1.7	n.s.
B: Migratory phase			
Body mass (g)/winglength ³ (mm) ($\times 10^{-6}$, \pm SD, n = 42, 39)	32.0 \pm 3.3	37.4 \pm 6.0	< 0.001
Increase in			
Body mass (g)/winglength ³ (mm) ($\times 10^{-6}$, \pm SD, n = 34, 29)	7.8 \pm 3.1	13.8 \pm 5.6	< 0.001

Most other studies examining the sunset orientation of migratory birds have emphasized the primary importance of solar-related information, either by artificially changing the position of the setting sun (KRAMER 1950; MOORE 1982, 1985; SANDBERG, in press), skylight polarization patterns (ABLE 1982, 1989; MOORE 1986; MOORE & PHILLIPS 1988; HELBIG & WILTSCHKO 1989), or by considering the seasonal shifts of the sunset azimuth (KATZ 1985).

Taken together, the existing evidence prompted us to design an experimental study to investigate if an unobstructed view of the setting sun and/or the associated skylight polarization patterns is of vital importance for selecting a seasonally appropriate migratory direction. The results clearly show that Scandinavian wheatears, when tested with an almost unrestricted view of the twilight sky, are able to select migratory directions that are in good agreement with ringing data (comp. Figs. 1 and 3). In contrast, when the visible sky section was reduced to 90° (\pm 45° from zenith), the wheatears oriented in seasonally inappropriate directions towards WNW. Tests performed under screened and unscreened conditions in Greenland indicated a similar influence of the amount of visible sky sector on the wheatears' orientation as found in Scandinavian birds. Without screens the Greenland wheatears failed to show a significant mean orientation, but the sample size was small.

These results, obtained with migratory wheatears tested under widely different natural geomagnetic conditions in Sweden and Greenland, respectively, confirm those described for nocturnally migrating North American emberizines, for which it has been repeatedly shown that an unrestricted view of the setting sun, and associated cues, is of crucial importance in the process of selecting a migratory direction (reviewed by MOORE 1987; ABLE 1989). This behaviour is

also similar to the autumn orientation of robins that were captured in South Sweden before crossing the Baltic Sea and subsequently tested under clear sunset skies (SANDBERG, in press). The robins preferred a mean direction towards the average sunset azimuth when tested with screens (90° sky section) clearly different from the expected southwesterly autumn direction revealed by ringing recoveries (SANDBERG et al. 1988a). On the other hand, when the birds were allowed to see approx. 160° of the sky above, including the lower parts of the sunset sky, they chose headings in good agreement with the angular distribution of ringing recoveries.

We have no answer to the question why an unobstructed view of the twilight sky, including the lower parts close to the horizon, assumes such importance for the wheatears (and the abovementioned robins) to orient in the migratory direction. Perhaps the W-NW orientation under screened conditions represents a fairly trivial response by birds, finding themselves in positions where part of the sky is blocked from vision, to seek a free view of the sunset sky at the time of departure (COCHRAN 1987). However, this offers no explanation for the wheatears' adherence to the same west-northwesterly mean directions under simulated total overcast, by their magnetic compass (SANDBERG et al., in press). Maybe the birds need the horizon line as a reference for correct orientation according to their visual and/or magnetic compass senses (see also PHILLIPS & WALDVOGEL 1982)? This is contradicted by magnetic orientation in the normal migratory direction shown by robins, in screened tests under clear as well as solid overcast skies, with previous experience of an extensive sea crossing (SANDBERG et al. 1988b). These conflicting results indicate the interesting possibility that there may be differences in the way geomagnetic and visual directional information is integrated at the beginning of the first autumn migration and during the subsequent actual (long distance) migration.

Release experiments, where both Scandinavian and Greenland wheatears were tested for directional preferences under free-flying circumstances, show that both categories of wheatears were able to select seasonally correct migratory directions when released under clear starry skies (see Fig. 1). The flight behaviour and vanishing intervals were very similar at the two release sites, and in particular, both samples chose departure directions in excellent agreement with existing ringing data (comp. Figs. 1 and 3). Greenland wheatears preferred directions that suggest a direct flight across the inland ice (ALERSTAM et al. 1986, 1990) and then continuing across the Atlantic towards southwestern Europe. The observed differences in the amounts of stored migratory body reserves between Greenland and Scandinavian birds (Table 1) indicate that the former indeed perform these extraordinary non-stop migratory flights.

In addition, the near significant difference in success rate (proportion departing on migratory flights) between released Scandinavian (90 %) and Greenland (61 %) passage migrants may suggest a stronger dependence on favourable weather conditions on the one hand, and an acute necessity to store enough migratory fuel on the other hand, for Greenland wheatears.

Release experiments, conducted under total overcast, indicated that Greenland wheatears were able to select a seasonally accurate migratory direction in the

absence of stars (see Fig. 2). The only difference between releases under clear starry skies and total overcast, respectively, was an increase in vanishing intervals (29 % longer under overcast skies), including more extensive circling before actual take-off. However, the difference in vanishing time was not statistically significant ($p > 0.05$, Mann-Whitney U-test). These results suggest that the birds, under solid overcast skies, may have used geomagnetic cues and that these cues were sufficient for selecting an appropriate migratory course.

Similar Orientation by Scandinavian and Greenland Wheatears

The results presented in this study show remarkable similarities between orientation responses to visual celestial cues in the twilight sky between migratory wheatears from Greenland and Scandinavia. Such a close similarity in orientation behaviour also holds true with respect to the wheatears' response to experimental manipulations of geomagnetic cues (SANDBERG et al., in press). This resemblance is surprising because the preconditions for visual as well as magnetic orientation differ considerably between S Sweden and W Greenland. The Greenland test site, located at a high geographic and geomagnetic latitude, has special implications for the birds' ability to acquire a functional sun compass, and also for the use of a magnetic compass in an area close to the North Magnetic Pole (ALERSTAM et al. 1990). Similarly, birds breeding in polar regions do not experience starry skies until shortly before the start of autumn migration, in contrast to migratory birds breeding at lower latitudes which have ample opportunities to develop their star compass already as nestlings/fledglings (EMLEN 1970).

In spite of these different orientation premises, our results indicate that the wheatears use basically the same compass system in the two areas. It still remains to be clarified how the birds' responses to manipulations of visible sky sections, and to experimental changes of geomagnetic cues, should be interpreted. The question of how visual and magnetic cues are integrated in the wheatears' orientation system, allowing successful migratory orientation at such widely different geographic and magnetic latitudes is fascinating and clearly warrants further research.

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