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Orientation and autumn migration routes of juvenile sharp-tailed sandpipers at a staging site in Alaska

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SUMMARY

Arctic waders are well known for their impressive long-distance migrations between their high northerly breeding grounds and wintering areas in the Southern hemisphere. Performing such long migrations requires precise orientation mechanisms. We conducted orientation cage experiments with juvenile sharp-tailed sandpipers (*Calidris acuminata*) to investigate what cues they rely on when departing from Alaska on their long autumn migration flights across the Pacific Ocean to Australasia, and which possible migration routes they could use. Experiments were performed under natural clear skies, total overcast conditions and in manipulated magnetic fields at a staging site in Alaska. Under clear skies the juvenile sharp-tailed sandpipers oriented towards SSE, which coincides well with reported sun compass directions from their breeding grounds in Siberia towards Alaska and could reflect their true migratory direction towards Australasia assuming that they change direction towards SW somewhere along the route. Under overcast skies the sandpipers showed a mean direction towards SW which would lead them to Australasia, if they followed a sun compass route. However, because of unfavourable weather conditions (headwinds) associated with overcast conditions, these south-westerly directions could also reflect local movements. The juvenile sharp-tailed sandpipers responded clearly to the manipulated magnetic field under overcast skies, suggesting the use of a magnetic compass for selecting their courses.

Key words: orientation, bird migration, sharp-tailed sandpiper, *Calidris acuminata*, Alaska.

INTRODUCTION

Arctic breeding waders are well known for their spectacular long-distance migrations between their summer and wintering areas (Morrison, 1984). Some species migrate over 10,000 km every spring and autumn, and some even make single non-stop flights that cover several thousand kilometres (Morrison, 1984; Pienkowski and Evans, 1984; Gill et al., 2009). Performing such long migrations and non-stop flights requires precise orientation mechanisms. Birds have been shown to use a number of different compasses for orientation during migration. They use a magnetic compass based on the inclination angle of the geomagnetic field, as well as celestial compasses that translate information from the azimuth position of the sun, the polarization pattern of skylight and the rotating stars into a migratory direction (for reviews, see Emlen, 1975; Able, 1980; Wiltschko and Wiltschko, 1995). The sun compass may be used with or without time compensation by the birds' internal circadian clock for the apparent motion of the sun during the day, over the year and at different geographic positions (Kramer, 1957; Schmidt-Koenig, 1990; Alerstam and Pettersson, 1991). Still, we have limited understanding of which compass systems birds use during migratory flights.

The routes taken by migrating birds may be based on at least two types of routes – orthodromes and loxodromes (e.g. Gudmundsson and Alerstam, 1998). The orthodrome, or great circle route, is the shortest route between two points on the Earth's surface, but requires continuous course changes as the birds move across longitudes (Snyder, 1993). The loxodrome usually represents a longer distance, but may be convenient from an orientation point of view because it is associated with a constant compass course (Snyder, 1993). Birds orienting by different orientation cues are led along different migration routes: (A) birds using their magnetic compass and following a constant magnetic course will migrate along magnetic loxodromes; (B) birds orienting by time-independent celestial cues (like the star compass, a sun compass constantly compensated for the latitudinal time shift along the route) or a magnetic compass regularly calibrated by sunrise/sunset cues (Muheim et al., 2006b) will travel along geographic loxodromes; (C) following a sun compass without compensating for the time-shift when moving across longitudes and making orientation decisions solely at sunrise and/or sunset will lead birds along great circle routes (Alerstam and Pettersson, 1991); or (D) following a sun compass without compensating for the time-shift when moving across longitudes but making the orientation decisions at various times of the day will lead the birds along more curved routes. In addition, orientation in relation to topographical cues (Gudmundsson et al., 1995) or wind (Green et al., 2004), as well as programmed changes in preferred compass courses (Gwinner and Wiltschko, 1978; Gwinner and Wiltschko, 1980), will affect the resulting migratory routes. There are indications that waders follow both loxodromes (Alerstam et al., 1990; Gudmundsson, 1994) and orthodromes (Alerstam and Gudmundsson, 1999; Alerstam et al., 2001; Alerstam et al., 2007) during migration depending on different environmental conditions such as latitude, topography, wind and weather conditions, food availability and stopover sites associated with different flight paths (Alerstam, 2001).

Our knowledge of the mechanisms of migratory orientation originates largely from orientation cage experiments performed mainly with nocturnally migrating passerines. Even though waders have been shown to be suitable for orientation cage experiments, there have only been three publications on the orientation behaviour of this group of birds in cages (Sauer, 1963; Sandberg and Gudmundsson, 1996; Gudmundsson and Sandberg, 2000).

The sharp-tailed sandpiper (*Calidris acuminata* Horsfield 1821) is a long-distance migrant breeding in northern Siberia and wintering mainly in Australia (Higgins and Davies, 1996). Adult and juvenile birds follow different migration routes during autumn migration. Adults migrate south to south-east from their breeding sites down to Australia while many of the juvenile birds migrate to staging areas in Alaska, from where they probably fly non-stop across the Pacific Ocean down to Australia (Tomkovich, 1982; Higgins and Davies, 1996; Handel and Gill, 2010). The aim of our study was to examine the migratory orientation of juvenile sharp-tailed sandpipers captured during autumn migration at a staging site in Alaska. The orientation data were then used to evaluate different migratory routes (sun compass routes, geographic or magnetic loxodromes), which the birds might use during their long-distance flights. We also examined whether the birds possess and make use of a magnetic compass during migration by performing orientation cage experiments in manipulated magnetic fields.

MATERIALS AND METHODS

Study species

We captured juvenile sharp-tailed sandpipers during autumn migration in the Yukon–Kuskokwim Delta in SW Alaska, a highly important staging and stopover area for large numbers of migrating tundra birds (e.g. Gill and Handel, 1990; Gill and Senner, 1996). Sharp-tailed sandpipers breed in northeastern Siberia from the Lena River in the west to the Kolyma River in the east (Higgins and Davies, 1996) (Fig. 1). Both adult and juvenile birds winter in Australasia from New Guinea and Tonga south to New Caledonia, Australia and New Zealand (with SE Australia holding most of the wintering population) (Higgins and Davies, 1996), but the two age groups have different autumn migration routes (Handel and Gill, 2010), which is rather unique among migrating birds (cf. Hake et al., 2003). In autumn, adult sharp-tailed sandpipers migrate on a broad front from their breeding grounds across eastern Siberia and continue overland and along the coast to south-east Asia. From there they migrate over water south across western Micronesia and the Philippines to their winter quarters in Australia (Tomkovich, 1982; Higgins and Davies, 1996), where they arrive from mid-August onwards, with the majority arriving in the first half of September (C. Minton, personal communication). The majority of the juvenile birds migrate from their site of birth to Alaskan staging grounds, where they arrive from mid-August onwards and stay until as late as mid-November (Higgins and Davies, 1996; Handel and Gill, 2010). From here they probably fly non-stop directly south through central Oceania to their Australian wintering grounds (Handel and Gill, 2010). Besides the staging areas in the Yukon–Kuskokwim Delta, they have also been observed at staging/stopover sites on the Alaska Peninsula and Aleutian Islands (Gill and Jorgensen, 1979; Handel and Gill, 2010).

Study site and experimental procedure

We carried out the orientation cage experiments at Kanaryarmiut Field Station (61°21′N, 165°08′W) in the Yukon–Kuskokwim Delta, SW Alaska, in September 2005 (Fig. 1) during the Swedish research expedition ‘Beringia 2005’ (Rickberg, 2006). Kanaryarmiut Field Station is located inland approximately 25 km from the coast near the Aphrewn River and the site consists of upland heath tundra (Nebel and McCaffery, 2003). Between 5th and 17th September, sharp-tailed sandpipers were caught at a camp site located on the coast, 30 km WSW (248°) of our testing site, using ‘Ottenby traps’ (Lindström et al., 2005). At capture, the birds were ringed, measured and weighed (to the nearest gram). Fat score was determined using a 9-grade scale for visual fat classification developed by Pettersson and Hasselquist (Pettersson and Hasselquist, 1985) (grades 0–6), and extended at Falsterbo Bird Observatory (grades 7–9). The age of the birds was identified on the basis of plumage characteristics (Prater et al., 1977). The birds were put into cardboard boxes after capture and transported either by float-plane or by motorboat from the capture site to the field station. There, they were kept in a large white tent (Hansen Weatherport Inc., Delta, CO, USA), allowing the birds to experience the natural photoperiod and ambient temperature, but no outdoor celestial cues. Up to five birds were kept in the same spacious non-magnetic cage (50 cm×100 cm×50 cm) with unlimited food (mealworms and fish pellets) and water with vitamins. Individual birds were held in captivity for between 4 and 16 days and used in orientation experiments up to five times

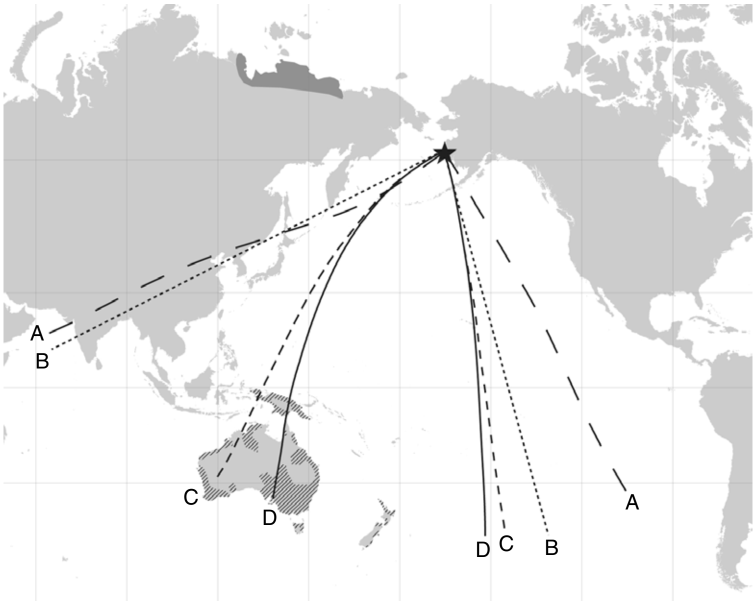

Fig. 1. Extrapolations of migration routes (total length of 12,000 km) of juvenile sharp-tailed sandpipers from the staging area in the Yukon–Kuskokwim Delta in SW Alaska (star), assuming the following compass mechanisms: (A) magnetic compass route following magnetic loxodromes; (B) sun compass route, with compensation for longitudinal time shift, or star compass route following geographic loxodromes; (C) sun compass route, no compensation for longitudinal time shift – orientation decision at sunrise/sunset; (D) sun compass route, no compensation for longitudinal time shift – orientation decision at various times of day. The mean directions from the orientation experiments (overcast: routes to the left; clear sky: routes to the right) were chosen as starting directions: the directions relative to magnetic North for magnetic loxodromes and the directions relative to geographic North for the geographic loxodromes and sun compass routes. The breeding range of sharp-tailed sandpipers is shown in dark grey, the wintering areas are striped. The map is drawn in a Mercator projection.

but are only represented once in each diagram. All birds were released at Kanaryarmiut Field Station after the experiments.

We used modified 'Emlen funnels' (Emlen and Emlen, 1966) lined with typewriter correction paper (Tipp-Ex, BIC GmbH, Eschborn, Germany) (see Rabøl, 1979; Beck and Wiltschko, 1981) to record the birds' migratory orientation. The orientation cages were made of non-magnetic materials, and the tops of the cages were covered with fine-mesh plastic netting allowing the birds to see approximately 160 deg. of the natural sky overhead. The directional tendencies of the birds were recorded by analysing the distribution of scratches left by the birds' claws on the pigment of the Tipp-Ex paper with a visual estimation method (see below).

Cloud cover was estimated visually at the beginning, middle and end of each experiment (0/8: cloudless; 8/8: completely overcast). Air pressure (in hPa), wind direction and velocity ($m\,s^{-1}$) were measured in the middle of each experiment with a hand-held weather station at the experimental site. We tested the directional preferences of the sharp-tailed sandpipers under both clear skies (1/8–6/8) and overcast conditions (naturally overcast when cloud cover was 8/8 or simulated overcast under partly cloudy skies, with opaque diffusing 3 mm Plexiglas sheets on top of the orientation cages).

To test for magnetic compass orientation, we used five pairs of electromagnetic coils (modified Helmholtz coils, 800 mm × 800 mm), powered by car batteries (12 V), to manipulate the local geomagnetic field. The orientation cages were placed in the centre of the coils where the magnetic field was most homogeneous [for technical specification of the coils see Sandberg et al. (Sandberg et al., 1988)]. We carried out experiments under two different magnetic conditions: (i) control condition: tests in the local geomagnetic field; and (ii) deflected condition: experiments with magnetic North (mN) shifted +90 deg. clockwise.

The orientation cage experiments were carried out between 6th and 20th September 2005, outdoors in a flat and open area without landmarks visible from within the orientation cages. Experiments lasted for 60 min and started within 1.5 h of local sunset, the time of day when many wader species normally initiate migration (Piersma et al., 1990; Alerstam et al., 1990; Gudmundsson, 1994). If a bird was inactive during the test hour, it was tested again until it showed activity. The elevation and azimuth of the sun in the middle of the experimental hour was calculated relative to geographic North using a computer program developed by the US Naval Observatory (USNO) Astronomical Applications Department (aa.usno.navy.mil). Experiments were performed at sun elevations varying between 8.1 and –3.9 deg. relative to the horizon. The local values of the geomagnetic field (declination +13 deg., inclination +72 deg., total field intensity 54,400 nT) were calculated for 1st September 2005, using the WMM-2005 magnetic model (McLean et al., 2004).

Data analysis and statistics

To determine the orientation of individual birds, as recorded by scratches in the pigment of the Tipp-Ex paper, we visually estimated the median direction to the nearest 5 deg. (Rabøl, 1979; Rabøl, 1995; Mouritsen, 1998). This method has been shown to be fast, highly repeatable and in close agreement with the more conventional method of counting the scratches in different sectors across the Tipp-Ex paper (Mouritsen and Larsen, 1998). The result of a given experiment was included only if at least 40 scratches were visible on the Tipp-Ex paper. Each paper was given a score between 0 and 4 for activity (0: <40 scratches, 1: 40–100, 2: 101–500, 3: 501–2000, 4: >2000) and concentration (indicates the angle within which the mean direction without doubt lies; 0: >45 deg., 1: 21–45 deg., 2: 11–20 deg., 3: 6–10 deg., 4: 0–5 deg.). Only if both scores had a value of at least one and if the sum of the two scores was at least three was the result included. This ensured that disoriented and unreliable orientation results were excluded. In total we excluded seven experiments carried out at high wind speeds (>7 $m\,s^{-1}$; 15th September) and four individuals tested during experiments performed during precipitation (17th September). Individual bearings were used to calculate a sample mean direction (α) and mean vector length (r) using vector addition according to standard procedures (Batschelet, 1981). The vector length (r) describes the scatter of the circular distribution (ranges between 0 and 1, the scatter being inversely related to the vector length). The Rayleigh test was used to test for significant directional preferences (Batschelet, 1981). Differences in mean angles between test categories were analysed by applying the one-way classification test ($F_{1,\mathrm{d.f.}}$) (Mardia, 1972). To analyse whether the mean orientation differed from the direction of the sunset point in the middle of the test hour we used 95% confidence intervals (CI) according to Batschelet (Batschelet, 1981). We compared maps of sea-level pressure between different test days to locate low-pressure centres in the area using data from the NCEP/NCAR 40 year re-analysis project (Kalnay et al., 1996). Differences in air pressure between clear sky and overcast conditions were analysed with Mann–Whitney U^2-test (Quinn and Keough, 2002), using SPSS (Chicago, IL, USA) v. 14.0. The significance level was set at $P<0.05$.

Simulation of compass routes

To analyse potential migration routes followed by juvenile sharp-tailed sandpipers, we used the mean directions chosen by the birds in the orientation experiments and extrapolated different migration routes based on these directions. We assumed the following compass mechanisms: (A) magnetic compass route following magnetic loxodromes; (B) sun compass route, with compensation for longitudinal time shift, or star compass route following geographic loxodromes; (C) sun compass route, without compensation for longitudinal time shift – orientation decision at sunrise/sunset; (D) sun compass route, without compensation for longitudinal time shift – orientation decision at various times of day. The extrapolations were carried out with routines written in MatLab (v. 7.6.0, R2008a, MathWorks, Natick, MA, USA), using the mapping toolbox 2.7.1 (MathWorks) and the magfd.m file by M. A. Tivey, Woods Hole Oceanographic Institution. Migration directions were recalculated for each step of 50 km for 240 steps (12,000 km). To calculate the changing declinations along the magnetic compass courses, we used geomagnetic data from the International Geographic Reference Field at the middle of the testing period (18th September 2005, IGRF 2005). We took the mean directions from the orientation experiments relative to magnetic North as the starting direction to extrapolate magnetic loxodromes and the mean directions relative to geographic North to extrapolate geographic loxodromes and sun compass routes [for methods see Muheim et al. (Muheim et al., 2003)]. The migration routes were illustrated with the help of ArcGIS (v. 9.1, Redlands, CA, USA) in a Mercator projection (Gudmundsson and Alerstam, 1998).

RESULTS

Orientation in the natural magnetic field

Sharp-tailed sandpipers tested in the local geomagnetic field under clear skies selected a mean direction towards geographic SSE (165±40 deg.; corresponding to 152 deg. relative to magnetic North; Fig. 2A), which is significantly different from the sun azimuth in the middle of the experimental hour (α=274 deg., $P<0.05$). Birds tested under natural and simulated overcast conditions showed a

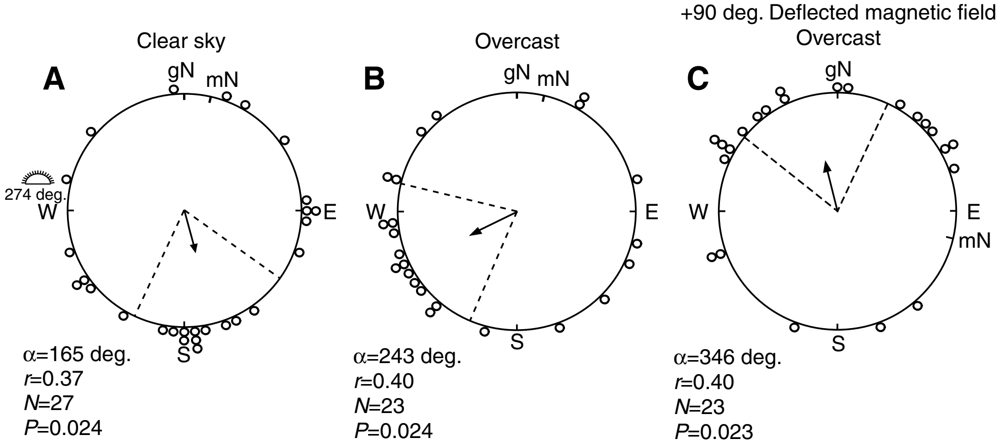

Fig. 2. Mean orientation of migratory juvenile sharp-tailed sandpipers under clear and overcast skies in the Yukon–Kuskokwim Delta, south-western Alaska in autumn. Each circle at the periphery of the diagrams represents the mean direction of one individual bird during one experimental hour (each individual is only represented once in each diagram). Individual mean headings are shown in relation to geographic North (gN) and magnetic North (mN). Experiments were conducted in the local geomagnetic field (A,B) and in a +90 deg. deflected magnetic field (C). The sun indicates the mean position of the setting sun in the middle of the experimental period. The mean vector (α) of each sample is illustrated by an arrow surrounded by the 95% confidence interval (dotted lines). Arrow lengths are proportional to the mean vector lengths (r) and are drawn relative to the radius of the circles (radius=1). Significance levels (P) are according to the Rayleigh test (Batschelet, 1981).

significant mean direction towards magnetic SW (230±40 deg., corresponding to 243 deg. relative to geographic North; Fig. 2B), which is significantly different from the mean orientation recorded under clear skies (comparison between directions relative to geographic North: $F_{1,48}$=6.65, P=0.013).

Orientation in a +90 deg. deflected magnetic field

In the +90 deg. deflected magnetic field under overcast skies, the sharp-tailed sandpipers responded by shifting their orientation accordingly (+103 deg. shift in mean orientation; Fig. 2C). The mean orientation in the deflected magnetic field (346 deg. relative to geographic North) was significantly different from the control direction under overcast conditions (243 deg. relative to geographic North; $F_{1,44}$=11.1, P=0.002). The average individual magnetic responses of the birds relative to their own control orientation (individual control direction=0 deg.) was 81 deg., which was close to the expected +90 deg. shift (included within the 95% CI of the mean direction of 81 deg.; Fig. 3).

Simulated migration routes

The extrapolations from the south to south-easterly starting directions observed during the clear sky experiments all lead to the South Pacific, indicating that neither of the sun compass routes nor the geographic or magnetic loxodrome routes leads the birds to their expected wintering areas in Australia (Fig. 1). Similarly, the migration routes following a magnetic or geographic loxodrome along the south-westerly starting directions chosen under overcast conditions do not direct the birds to Australia, but through China and India towards Africa (Fig. 1). The two sun compass routes under overcast conditions with no compensation for longitudinal time shift, on the other hand, guide the birds down to their wintering areas in Australia (Fig. 1).

Analysis of pressure and winds

The NCEP/NCAR re-analysis dataset showed that the regional sea-level pressure differed considerably between clear sky and overcast days. On clear sky days the centre of the low-pressure was located over inland Alaska, east of our experimental site, while on overcast days the centre was over the Bering Sea, west of our site. The mean air pressure during clear sky experiments was 1013.2 hPa (range: 1001.7–1015.8 hPa), significantly higher than the mean air pressure during the overcast experiments (1001.8 hPa, range: 992.5–1018.9 hPa; Z=–2.72, P<0.01, Mann–Whitney U^2-test). The mean wind direction differed significantly between experiments conducted under clear skies (α=333 deg., north–north-westerly winds, r=0.99, N=27, P<0.05) and overcast conditions (α=204 deg., south–south-westerly winds, r=0.79, N=23, P<0.05; $F_{1,48}$=227, P<0.001).

DISCUSSION

Difference in orientation between clear skies and overcast condition

We found a clear difference between the mean orientation of the juvenile sharp-tailed sandpipers tested under clear sky and overcast conditions, suggesting different course preferences related to the visibility of celestial cues and/or local weather conditions.

Birds tested under clear skies chose south to south-easterly directions, whereas birds tested under overcast conditions oriented towards the south-west. From an orientation point of view, we would not expect a difference in orientation, as birds are expected to calibrate all of their compasses, i.e. so they conform with a common reference, during a stopover (see Muheim et al., 2006b).

We found that the orientation recorded under overcast compared with clear sky conditions was related to a difference in air pressure and wind conditions during these tests (i.e. location of the low-pressure centres in relation to the test site resulted in either tail or headwinds and differences in air pressure). High or increasing air pressure typically occurs after the passage of cyclones, which arrive from the west in Alaska, resulting in good flight conditions (tailwinds and decreasing cloud cover) for southward migration (Richardson, 1982; Alerstam, 1990; Åkesson and Hedenström, 2000). Birds have been shown to be able to detect small differences in air pressure (Kreithen and Keeton, 1974), and presumably air pressure changes can be used to predict favourable flight conditions for migration (Richardson, 1982; Alerstam, 1990; Åkesson et al., 2002). Satellite tracking of bar-tailed godwits (*Limosa lapponica*

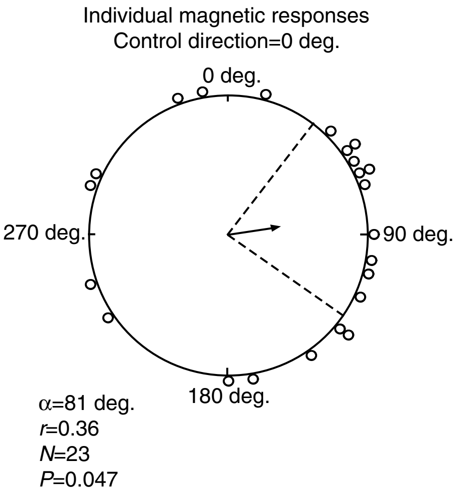

Fig. 3. Magnetic response of individual birds after exposure to a +90 deg. deflected magnetic field. Control direction (Fig. 2B) of each individual bird is set to 0 deg. For further information see Fig. 2.

baueri) shows that the birds depart from Alaska on the back of low-pressure systems approaching Alaska from west to south-west, catching the counter-clockwise winds directing them south to south-east (Gill et al., 2009). All godwits departed when the low-pressure centre was located east of their departure site in western Alaska (generating tailwinds) while no birds departed when the low-pressure centre occurred west of the departure site [generating headwinds (Gill et al., 2009)]. Bar-tailed godwits, as well as other bird species migrating from Alaska (e.g. Warnock and Gill, 1996; Gill et al., 1997), have probably evolved this wind-sensitive migration strategy associated with the Aleutian low pressure system, which shapes and dominates weather and wind patterns in the North Pacific (Gill et al., 2005).

Orientation under clear skies

Our clear sky experiments were all conducted when the Aleutian low-pressure centre was located east of the test site, generating tail-winds from NNW, indicating that these were days when southward migration could commence with wind assistance. It is therefore probable that juvenile sharp-tailed sandpipers also use these winds associated with the Aleutian low-pressure system for their southward migration and thus are able to detect changes in air pressure resulting in favourable flight conditions (i.e. tailwinds) for their southward migration. If so, the high air pressures measured during the clear sky experiments seem to have triggered orientation responses towards the wintering areas, similar to those observed for other waders wintering in Australia and nearby islands (Gill et al., 2009), while the lower air pressures during the overcast experiments might have triggered local movements (see also discussion below). However, the south to south-easterly direction shown in our clear sky experiments also corresponds well with the expected directions that would take the birds to known staging areas further south on the Alaska Peninsula and Aleutian Islands. Many sharp-tailed sandpipers depart from these more southerly staging sites on their long non-stop flights across the Pacific Ocean to Australia, but to what extent birds are moving from the Yukon–Kuskokwim Delta to these more southerly staging grounds is not known (Handel and Gill, 2010). Over-seas departures from further south will reduce flight distance by at least 600 km compared with departure from staging sites on the Yukon–Kuskokwim Delta, but high body masses of birds on the Yukon–Kuskokwim Delta suggest that birds are able to embark on migration to Australia from this more northerly staging site (Å. Lindström, personal communication). It is probable that the local wind conditions during these flights as well as the physiological state of the birds and foraging conditions in the Yukon–Kuskokwim Delta will influence the decision whether to initiate the long migration flights further north or south (e.g. Åkesson and Hedenström, 2007).

Orientation under overcast skies

The south-westerly mean orientation of the juvenile sharp-tailed sandpipers observed under overcast conditions differed from the orientation recorded under clear sky conditions. Several studies have shown that migratory waders are less motivated to depart from stopover sites under overcast skies (Piersma et al., 1990) and all orientation studies with waders published so far have shown that the birds were inactive, disoriented or showing a bimodal distribution of preferred headings when tested under overcast conditions (Sauer, 1963; Sandberg and Gudmundsson, 1996; Gudmundsson and Sandberg, 2000). In our experiments the juvenile sharp-tailed sandpipers tested during overcast conditions were as active as under clear sky conditions and showed a significant mean orientation towards SW indicating that they did not have a problem orientating under overcast conditions. The Aleutian low-pressure centres were situated west of our study site during overcast tests, generating headwinds from SSW, making these days less advantageous for southward migration compared with the clear sky days with tailwinds from the north. Although several factors, such as the presumably limited possibility of sun compass orientation under overcast conditions (cf. Hegedüs et al., 2007), the general reduction in migratory motivation and presence of headwinds, speak against the idea that the south-westerly direction shown in our overcast experiments is the juvenile sharp-tailed sandpipers true migratory direction, we cannot exclude this as a possibility.

An alternative explanation for the south-westerly direction shown in our overcast experiments could be that the birds were showing a compensatory behaviour caused by local movements. The sharp-tailed sandpipers were tested after a displacement of about 30 km, and the direction of the trapping site (248 deg.) is very close to the mean orientation (243 deg.) recorded for the birds under overcast skies. The birds may compensate for the local experimental displacement, perhaps trying to get back to the trapping site, because it is a profitable foraging area for waders and one which the experimental birds were exploring for refuelling (Å. Lindström, personal communication) prior to capture. In that sense, their cage activity under overcast conditions would probably not be migratory activity, but instead some sort of local movement to return to good foraging sites. If this is the case it suggests that experimental birds could navigate and orient their activity in the cages towards the last known site they visited before the displacement. Similar orientation of local movements (3–19 km) selected relative to the magnetic field have been shown under overcast conditions for displaced juvenile barn swallows (*Hirundo rustica*) reorienting to roost sites explored during autumn migration (Giunchi and Baldaccini, 2006).

Effects of magnetic field manipulations on orientation

We found that the sharp-tailed sandpipers closely followed a +90 deg. shift of the horizontal component of the magnetic field around the funnels, on an individual as well as a group level, indicating that they use the geomagnetic field for orientation. A magnetic compass has previously been demonstrated only for one species of waders, the sanderling (*Calidris alba*) (Gudmundsson and Sandberg, 2000).

Orientation in view of possible migration routes

Orientation under clear skies

Our extrapolations of alternative migration routes clearly show that neither of the sun compass routes nor geographic or magnetic loxodrome routes following the south to south-easterly starting direction expressed under clear sky tests will lead the birds to their expected wintering areas in Australia (Fig. 1), unless they shift course during their migration. Such a course shift has recently been reported for bristle-thighed curlews (*Numenius tahitiensis*) and Alaskan bar-tailed godwits during their non-stop trans-Pacific autumn migration to Oceania and New Zealand, respectively (McCaffery, 2008; Gill et al., 2009). After leaving Alaska in south to south-easterly directions they are expected to encounter clockwise winds near Hawaii, which redirect them south to south-west towards their wintering grounds (McCaffery, 2008; Gill et al., 2009). Regular observations of juvenile sharp-tailed sandpipers from the Hawaiian Archipelago during autumn (Pratt et al., 1987; Handel and Gill, 2010) support this idea of redirected flights possibly caused by winds. It might be that the juvenile sharp-tailed sandpipers use adaptive wind drift to reach their wintering areas as has been reported for other arctic waders (Green et al., 2004). Adaptive wind drift predicts initial drift during the migratory journey, followed by compensation during later stages as the birds are approaching their destinations (Alerstam, 1979; Green et al., 2004). With stable wind systems along the migratory route the juvenile sharp-tailed sandpipers might not need to change their heading until the end of the journey which means that they could continue to fly in their south-easterly direction and let the wind redirect them to the south-west as they approach Hawaii.

If the south to south-easterly starting direction shown in our clear sky experiments is the true migratory direction of the juvenile sharp-tailed sandpipers and we assume that they redirect their orientation to the south-west on the route, we cannot in principle exclude any of our suggested compass routes. Arctic waders have been suggested to follow sun compass routes (without compensating for the time shift when travelling across longitudes) between high Arctic breeding areas and their wintering grounds (Alerstam et al., 2001). Thus, are the juvenile sharp-tailed sandpipers following a sun compass route (Alerstam and Pettersson, 1991) from their birth places in northern Siberia to their staging areas in Alaska and during their migration further south? Several Arctic breeding wader species have been suggested to migrate along sun compass routes between Siberia and North America (Alerstam and Gudmundsson, 1999; Alerstam et al., 2001; Alerstam et al., 2007). Studies carried out in northern Siberia and in the Bering Strait during autumn migration show that most of the migrating birds (mainly waders) were travelling in easterly directions from Siberia towards Alaska and migrants over the Bering Strait showed more south-easterly and southerly directions (Alerstam and Gudmundsson, 1999; Alerstam et al., 2007). If the juvenile sharp-tailed sandpipers followed a sun compass route (without compensating for the time shift when travelling across longitudes) from a centred location in their breeding area in northern Siberia to our study site in Alaska, they would start in a direction towards the east (90 deg. relative to geographic North), and end up in a south-easterly (136 deg. relative to geographic North) direction when arriving at the Yukon–Kuskokwim Delta. This south-easterly direction does not differ from the mean direction observed in our clear sky experiments (included within the 95% CI of the mean direction of 165 deg.) suggesting the possibility that the birds might be travelling along a sun compass route from Siberia to Alaska as well as during their migration further south. Furthermore, the sun compass routes direct the birds to the Hawaiian Archipelago where observations of juvenile sharp-tailed sandpipers are frequent (Handel and Gill, 2010). We cannot exclude the possibility that the birds change their compass mechanism during their staging in Alaska and rather than migrating on a fixed sun compass course divide their journey into differently programmed orientation steps to accomplish the course changes needed to reach their wintering areas. The staging period in Alaska is long enough to permit recalibration of compasses (e.g. Wiltschko et al., 1998; Muheim et al., 2006a), as well as adjustment of the internal clock to the local time, so in principle the two migration sections could be programmed and performed independently from each other. Furthermore, stars become visible to the birds in autumn as they reach more southerly latitudes, and experience from stars might be important to the birds before they depart on their several days long, non-stop flights across the Pacific Ocean. It is, however, interesting to note the striking similarity between these courses before and after staging at the Yukon–Kuskokwim Delta sites.

Orientation under overcast skies

A migration route starting in the south-westerly directions chosen by our juvenile sharp-tailed sandpipers under overcast conditions directs the birds through China and India towards Africa when following a magnetic or geographic loxodrome for more than 10,000 km (Fig. 1). Neither of these two routes is likely, as autumn findings of juvenile sharp-tailed sandpipers in these areas are very rare (Higgins and Davies, 1996; Handel and Gill, 2010). The sun compass routes starting with the courses recorded during overcast conditions with no compensation for longitudinal time shift, on the other hand, guide the birds near to their wintering areas in Australia (Fig. 1). Could these be possible migration routes for juvenile sharp-tailed sandpipers during autumn migration and is it possible for them to use their sun compass under overcast conditions? The degree of skylight polarization is reduced under overcast conditions, but the pattern of polarized skylight is very similar to the clear sky conditions, suggesting that polarized light could possibly also be used under partly covered and overcast skies to locate the position of the sun if the birds' sensory system is adapted to detect low degrees of polarization (<10%) (Hegedüs et al., 2007). However, it is still not known whether birds can perceive such low degrees of polarization under overcast skies (Horváth and Varjú, 2003). Because of unfavourable weather conditions (headwinds) associated with overcast skies, the south-westerly directions could also reflect local movements (see above).

LIST OF SYMBOLS AND ABBREVIATIONS

CI	confidence interval
gN	geographic North
mN	magnetic North
P	significance level
r	mean vector length
α	mean direction

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