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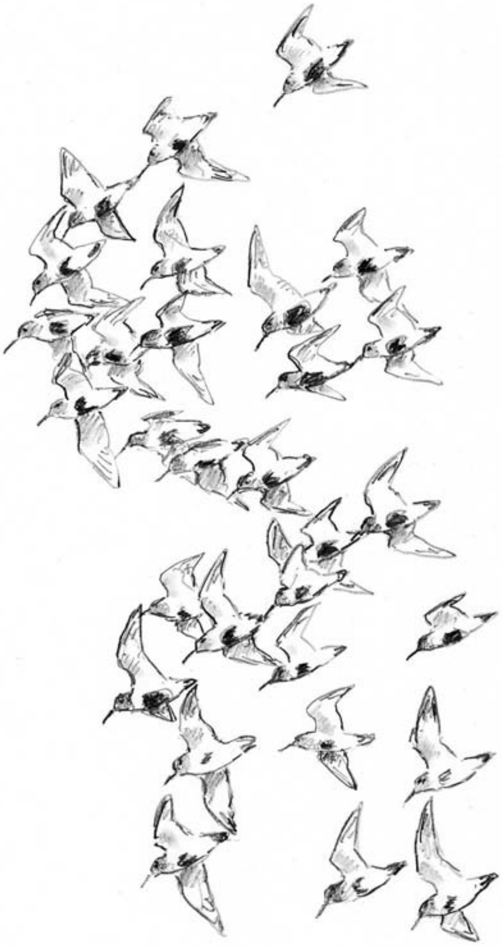
Fine-scaled orientation changes in migrating shorebirds

Johanna Grönroos[1,*], **Martin Green**[1] & **Thomas Alerstam**[1]



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Flight directions and routes of migrating birds are determined by the birds' compass orientation, but also by effects of wind, social influence, responses to topography and landmarks, and to navigation cues. We investigated the orientation and routes taken by arctic shorebirds during autumn migration in southern Sweden at three different sites situated within a distance of 200 km from each other, in relation to the birds' destinations. We used three different methods, visual telescope observations, tracking radar registration and ring recoveries. Mean track directions differed significantly between the different sites in a way that demonstrated fine-scaled orientation changes when the shorebirds passed the southern Baltic region. The gradual change cannot be explained by different wind conditions at the different sites or by distinct responses to specific topographical features, i.e. the birds were not following coastlines or prominent landmarks in any detailed way. Neither could it be reconciled with orientation according to any of the main compass mechanisms known to be used by migrating birds which indicates that the control of flight courses and paths may be more complex than expected. The shorebirds might travel within a slightly winding flight corridor in broad agreement with the large-scale topography to maximize general association with coastal habitats during migration. Juvenile birds had a significantly different orientation than adults, particularly when the juveniles travelled in flocks without any adults. Juvenile birds may learn the general flight paths and course changes in relation to the large-scale topography from older and experienced individuals in the flocks, but most of this learning process between generations probably does not take place until after the birds' first autumn migration.

Key words: migration, orientation, shorebird, tracking radar, ring recoveries

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Already in the nineteenth century Palmén (1874) noticed that shorebirds migrating from breeding grounds in Siberia migrated along well-defined routes towards their wintering grounds, and he also pointed to such well-defined routes in the southern Baltic Sea. Today some scientists consider these routes to be more like a 'migration highway' with shorebirds migrating on a rather broad front of several tens or hundreds of kilometres (Meltofte 2008). Most likely there are differences between different sub-populations and seasons as well as age-classes of birds in this respect. Sweden is situated along the East Atlantic Flyway, one of the major flyways of arctic shorebirds, where birds breeding in Siberia migrate to the North Sea region (mainly the Wadden Sea) during autumn to fatten up and/or moult before continued flights towards wintering grounds in both western Africa and western Europe. Spring migration of shorebirds flying along this route passing southern Sweden has been investigated (Gudmundsson 1994, Green 2004) but much less is known about autumn migration.

The routes taken by migrating birds may be based on at least two types of trajectories on the Earth's surface – orthodromes and loxodromes (e.g. Gudmundsson & 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. The loxodrome, or rhumbline, represents a longer distance, but may be convenient from an orientation point of view because it is associated with a constant compass course (Alerstam & Pettersson 1991, Snyder 1993). During spring migration shorebirds and geese passing south Sweden on their way towards the Russian tundra fly along routes clearly different from orthodromes and approximately in accordance with loxodromes (Gudmundsson 1994, Green *et al.* 2002, Green 2004). Less is known about autumn migration routes, and radar studies made along the coast of the Arctic Ocean during the initial part of the journey towards the North Sea region allow rejection neither of orthodromes nor of loxodromes (Alerstam & Gudmundsson 1999). Still, flights along loxodromes are inferred from the pattern of observed birds in the south Baltic region, also during autumn migration. If the main migration corridor followed along orthodromes, this would simply not lead to large numbers of shorebirds passing these areas (cf. Gudmundsson 1994, Green *et al.* 2002).

In spite of extensive knowledge about orientation and migration performance of birds, based on experimental behavioural studies of compass mechanisms, on displacement and homing experiments and on ringing and tracking studies (e.g. Newton 2008, Wiltschko & Wiltschko 2009) there is still a poor understanding of how birds orient when actually travelling on migration. We can assume that flight directions and paths of migrating birds are determined by the birds' compass orientation, but also by effects of wind, social influence (particularly for birds migrating in flocks), responses to topography and landmarks, and to navigation cues. To investigate how these different factors interact to control the flight paths of migrating birds, we need to carefully analyse the geometry of flight routes at different geographic scales, from small-scale orientation behaviour over short distances up to global journeys of tens of thousands of kilometres (Alerstam 1996).

The objective of this study was to investigate the orientation and routes taken by arctic shorebirds along the East Atlantic Flyway during autumn migration in southern Sweden at three different sites situated within a distance of 200 km from each other, in relation to the birds' destinations in the North Sea region. We used three different methods, visual telescope observations, tracking radar registration and ring recoveries to throw light on the autumn orientation of the shorebirds in the southern Baltic region. By investigating flight directions and orientation of shorebirds within a limited region of a few hundred kilometres, corresponding to only a few hours' flight time, we wished to test the following critical aspects of shorebirds' course control system:

(a) If the shorebirds followed constant compass orientation according to the sun-, star- or magnetic compass mechanisms during their passage of the southern Baltic region.

(b) If the shorebirds tended to follow curved flight paths with course changes in a similar way as demonstrated for Red Knots *Calidris canutus* passing the southern Baltic region during spring migration (Gudmundsson 1994). This would imply that flight paths across this region are determined by the same control mechanisms during spring and autumn migration.

(c) If orientation differed between adult and juvenile birds, which would suggest that learning and experience were involved in the course control.

METHODS

Flight directions

TELESCOPE TRACKING

Observations of migrating shorebirds were carried out during the period 26 July to 15 October in four years, 2006–08 and 2011 at Ottenby Bird Observatory (56°12'N, 16°24'E), situated on the southernmost point of the island of Öland (south-east Sweden) in the Baltic Sea (Figure 1). Observations were made during 41 days. The observation time each day was not standardised, but 84% of the observations were made between 17:30 and 20:30 h (Swedish summer time = GMT +2h) and 16% between 05:30 and 08:30. Migrating flocks were normally located by using 10× binoculars and later tracked in 20–60× telescopes until they vanished from sight. Telescopes were equipped with azimuth scales and were carefully aligned to give geographic compass bearings. The following data were recorded in order to determine track directions of the birds: (1) the compass bearing (b_1°), and (2) estimated horizontal distance (d_1) from the observer to the bird flock when the telescope tracking started – this normally occurred when the flock passed relatively near the observer; (3) the time of telescope tracking until the flock vanished from sight, and (4) vanishing bearing (b_2°). The flight distance covered by the birds during the time of tracking (d_2) was estimated by assuming that the birds travel with a speed of 16 m/s which is a normal flight speed of Dunlins *Calidris alpina* (which comprise 95% of the flocks, pers. obs.). The angle for parallax compensation (ε°) could be calculated from

$$\varepsilon = \arcsin\left[\frac{d_1}{d_2} \bullet \sin(b_1 - b_2)\right]$$

The flight direction of the flock is then determined as

($b_2 + \varepsilon$). The angle ε will be positive or negative depending on whether the flock passed to the left or right respectively of the observer facing the vanishing bearing. To avoid large errors in estimated flight directions we have only included observations with an effective tracking time of at least 1 minute. Mean tracking time was 2 min 35 s (with maximum 10 min 13 s) and mean absolute angle for parallax compensation was only 2.7° (0–11°). Estimated flight directions were robust in relation to potential bias caused by the parallax compensation or assumptions about airspeed (16 m/s). Restricting the analyses to include only flight directions with parallax angles less than 2° or changing assumptions about flight speed from 16 to 13 m/s (mean wind effect at Ottenby: –3 m/s) affected mean flight directions with only 0.5° which shows that track direction estimates are reliable with high accuracy. Heading directions were then calculated by subtracting the angle of compensation/drift (α) from track direction. Alpha (α) was calculated according to the following equation:

$$\alpha = \arcsin(a \sin \beta) ,$$

where a is the ratio between wind speed and the birds' airspeed (16 m/s) and β is the angle between track and wind direction (Alerstam 1976). All shorebird flocks were identified and belonged to the species Dunlin, Red Knot, Bar-tailed Godwit *Limosa lapponica*, Grey Plover *Pluvialis squatarola*, Ringed Plover *Charadrius hiaticula*, Turnstone *Arenaria interpres* and Sanderling *C. alba*. 85% of the flocks were composed of only Dunlins, 10% were flocks of mixed species including Dunlins (on average 51% of the individuals in the mixed flocks were Dunlins) and in 5% of the flocks there were no Dunlins but only other shorebird species. The birds in the flocks were aged (juvenile or adult) when observation conditions allowed.

RADAR TRACKING

Tracks of migrating flocks of shorebirds were recorded at two sites in Scania, South Sweden (Figure 1). Shorebirds were tracked with mobile tracking radar (X-band, 40 kW peak power, pulse duration 0.3 μs, pulse repeat frequency 1800 Hz, 2.2° pencil beam width) at Vitemölla at the Baltic Sea coast (55°42'N, 14°12'E) and Björka, in South Central Scania (55°39'N, 13°37'E) between 15 July and 25 September 1982, 1984, 1986, 1989 and 1990. The radar was operated manually and data about the range, elevation and azimuth of the flocks were recorded by a computer. Flocks of shorebirds were tracked from 1 up to 14 min. The range of the radar was about 15 km for large flocks and smaller flocks could be tracked at distances up to 10 km. To determine headings (the orientation of the birds' body axis) and airspeeds (the birds' flight speed relative to the surrounding air) of the flocks, wind direction and speed were measured by tracking helium-filled weather balloons carrying an aluminium foil reflector. Heading directions and airspeeds were then calculated by vector subtraction of wind velocity at the altitude at which the birds were flying from the birds' track vector over the ground (track direction and ground speed). For a more detailed description of radar tracking procedures see Alerstam (1985). All shorebird flocks were visually identified and belonged to the species Dunlin, Bar-tailed Godwit, Grey Plover, Ringed Plover, Red Knot and Turnstone. 53% of the flocks were composed of only Dunlins, 3% were flocks of mixed species including Dunlins (on average 67% of the individuals in the mixed flocks were Dunlins) and 44% of the flocks were composed of other shorebird species.

Migratory destination and origins

We obtained ringing recoveries of Dunlins ringed at Ottenby (see above) and Falsterbo (55°23'N, 12°50'E; Falsterbo Bird Observatory, south-western Sweden, Figure 3) during autumn migration and recovered during the same season (July to October) at a distance of at least 100 km. The dataset included 364 recoveries from Ottenby and 32 from Falsterbo. We calculated loxodrome (constant bearing between two geographical coordinates) directions between ringing and recovery sites. For the comparison between ringing recoveries and visual/radar data we removed recoveries from the southeasterly quadrant (<180°) since most probably none of the birds recorded in our study were birds with easterly destinations. A total of 16 easterly recoveries were removed. The ringing recovery data was analysed in the same way as the other results (see below). Mean direction of ring recoveries remained the same (changing by only one or two degrees) if we restricted the analysis to recoveries reported within 30 days from ringing ($n = 251$) or excluded all recoveries of birds shot ($n = 229$). This indicated that mean directions based on ringing were robust against possible biases associated with time after ringing or changing hunting pressure. Hence, we used the total available recovery sample from the months July to October (same season as ringing took place) for our analyses.

Dunlins migrating over southern Scandinavia in autumn originate from breeding areas in northern Europe and western Siberia as far east as Yamal peninsula (about 70°E, Fransson *et al.* 2008).

Data analysis and statistics

Calculations of mean directions and angular deviations of flight directions were made according to standard circular statistical methods (Batschelet 1981). The Rayleigh test was used to test for significant directional preferences and differences in mean angles between test categories was analysed with the Watson–Williams *F*-test (Batschelet 1981).

General linear model (GLM) analyses were performed using the statistical software SPSS version 18.0 (SPSS Inc., Chicago, USA) to test if track and heading directions differed significantly between sites and age groups independently of any effect of wind on the birds' flight directions. The effects of wind shown in these analyses were evaluated elsewhere; Grönroos *et al.*, unpubl. data. Track or heading direction was used as dependent variable, and for the tests of differences between sites, we used wind (wind from the left and right, fixed factor), site (fixed factor) and the interaction between wind and site as independent variables. For the tests of a difference in flight directions between age groups (data from Ottenby only) we used wind (fixed factor), age (three groups as fixed factor; flocks of adult birds, flocks of juveniles and mixed flocks with adults and juveniles) and the interaction between wind and age as independent variables. We are aware that GLM can provide only approximate tests since directions are not linear but circular data. Still such tests will be robust when directions are highly concentrated around a well-defined mean (80% of directions in all six samples of track directions were within ±26–37° from mean directions; see also Table 1 for angular deviations; Batschelet 1981) and sample sizes are reasonably large, as in our present cases (results with marginal significance must be considered with due care).

RESULTS

Flight directions

Summary statistics of flight/recovery directions for the different sites, methods and age classes are shown in Table 1. In all cases the migratory movements were concentrated with relatively little scatter (angular deviations ranging between 10 and 25 degrees).

Mean track directions differed significantly between Ottenby and Björka and Vitemölla and Björka (Watson–Williams *F*-test: $F_{1,207} = 14.0$, $P < 0.001$; $F_{1,72} = 4.4$, $P = 0.04$, respectively, Figure 1) but not between Ottenby and Vitemölla. Mean heading directions differed significantly between Ottenby and Vitemölla and between Ottenby and Björka (Watson–Williams *F*-test: $F_{1,215} = 16.3$, $P < 0.001$; $F_{1,207} = 31.2$, $P < 0.001$, respectively, Table 1) but not between Vitemölla and Björka. The GLM analysis confirmed that

Table 1. Flight and recovery directions for migrating shorebirds during autumn at four different sites in S Sweden, based on visual telescope tracking, radar tracking and ring recoveries. Average flight (track and heading) or recovery direction of each sample are shown together with angular deviations (A.D.).

Site	Method	Age	Track/Heading	Direction (°)	A.D. (°)	*n*
Ottenby	Visual	All	Track	234	16	176
			Heading	234	13	176
		Ad	Track	237	11	105
			Heading	233	10	105
		Mixed	Track	231	17	34
			Heading	238	14	34
		Juv	Track	218	22	19
			Heading	225	13	19
	Ring recovery	All		242	16	350
		Ad		245	15	150
		Juv		240	17	200
Vitemölla	Radar	All	Track	236	20	41
			Heading	243	17	41
Björka	Radar	All	Track	246	22	33
			Heading	250	25	33
Falsterbo	Ring recovery	All		245	17	30
		Ad		244	19	23
		Juv		249	10	7

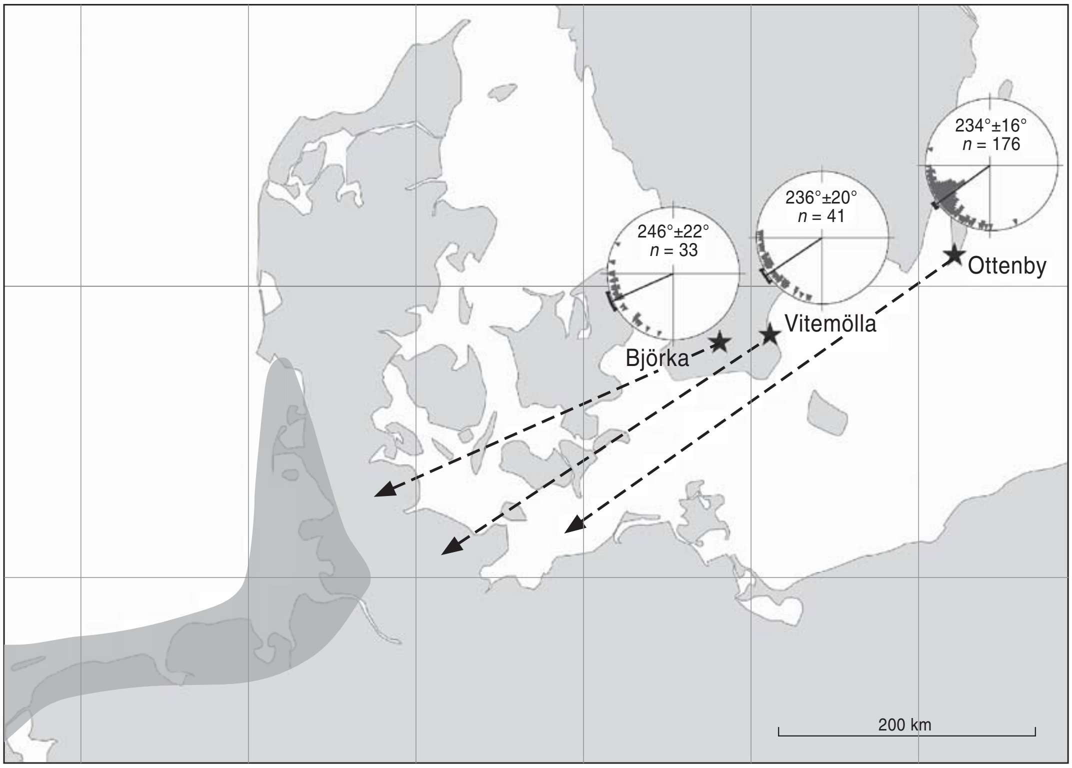

Figure 1. Mean track directions (± angular deviation) and number of trackings of shorebirds on autumn migration at three study sites in southern Sweden. Dark grey area represents the Wadden Sea. The map is a Mercator projection.

there was a significant effect of site on track and heading directions (GLM: $F_{2,244} = 10.0$, $P < 0.001$; $F_{2,244} = 7.8$, $P < 0.001$, respectively) independently of the effect of wind.

Mean track directions of shorebirds migrating from Ottenby differed significantly between age groups (Watson–Williams F-test: adult–juvenile: $F_{1,122} = 30.0$, $P < 0.001$, adult–mixed: $F_{1,137} = 6.7$, $P = 0.01$, juvenile–mixed: $F_{1,51} = 4.7$, $P = 0.034$, Figure 2). The mean direction of juvenile birds was more to the south compared to adults. Mean heading directions differed significantly between adult and juvenile flocks and between juvenile and mixed flocks (Watson–Williams F-test: $F_{1,122} = 9.9$, $P = 0.002$; $F_{1,51} = 9.6$, $P = 0.003$, respectively, Table 1) but not between adult and mixed flocks. GLM analyses confirmed that there was a significant effect of age on track directions (GLM: $F_{2,152} = 4.3$, $P = 0.016$) as well as on heading directions (GLM: $F_{2,152} = 3.5$, $P = 0.032$), independently of the effect of wind on the birds' flight directions.

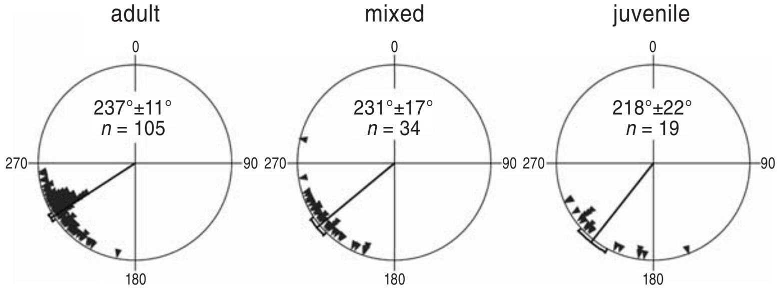

Figure 2. Mean track directions (± angular deviation) and number of trackings of migratory Dunlins at Ottenby, southern Sweden in autumn. Each triangle at the periphery of the diagrams represents the track direction of one flock.

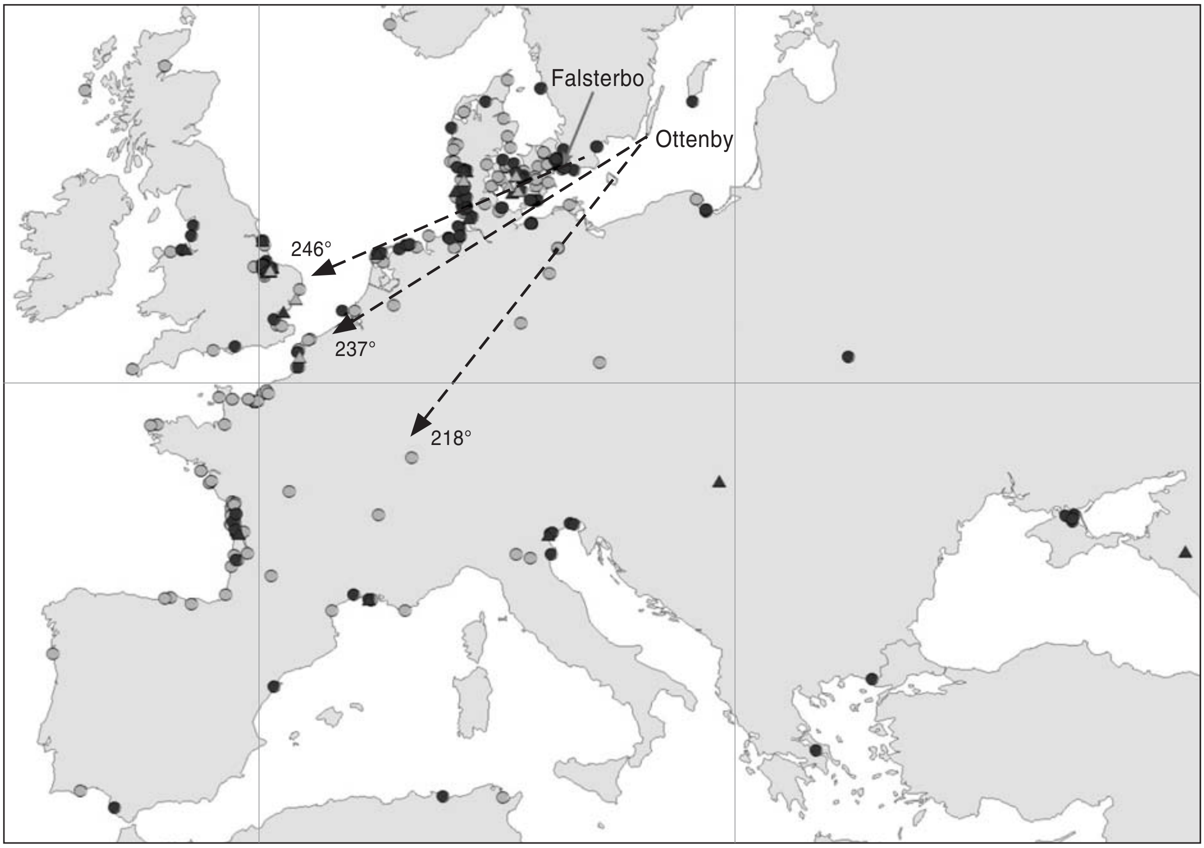

Figure 3. Recoveries of Dunlins ringed at Ottenby (circles) and Falsterbo (triangles) Bird Observatories in southern Sweden. Only birds ringed and recovered during the same autumn season (July to October) at a distance of at least 100 km are included. Black and grey symbols represent adult and juvenile birds, respectively. Dashed arrows show mean track direction of shorebirds from Björka (246°) and adult and juvenile Dunlins from Ottenby (237° and 218°, respectively) for comparison. The map is a Mercator projection.

Migratory destination and origins

A total of 396 Dunlins ringed at Ottenby and Falsterbo have been recovered during the same autumn season (July to October) at a distance of at least 100 km (Figure 3, Table 1 with easterly recoveries removed). There was no difference in mean directions between the recoveries of Ottenby and Falsterbo (Watson–Williams *F*-test: $F_{1,378} = 1.2$, $P = 0.27$, Table 1). Since ringing recoveries from Ottenby are in great majority (350 *versus* 30) and the fact that we found no difference in mean direction between Ottenby and Falsterbo we now compare our flight directions with ringing recoveries from Ottenby. There was a significant difference in mean migratory direction between visual track and heading observations and ringing recoveries from Ottenby (Watson–Williams *F*-test: $F_{1,524} = 28.2$, $P < 0.001$, $F_{1,524} = 34.1$, $P < 0.001$ respectively, Table 1). Birds observed passing Ottenby were on average migrating towards slightly but significantly more southerly directions in comparison with directions of ring recoveries.

Juvenile Dunlins ringed at Ottenby migrated with significantly more south-oriented directions compared to adult birds (Watson–Williams *F*-test: $F_{1,348} = 7.2$, $P = 0.008$, Table 1). Hence, both ringing recoveries and visual observations from Ottenby indicated that juvenile Dunlins migrate along more southerly directed routes compared to adults.

Based on ringing recoveries from the breeding region (Gromadzka 1989, Fransson *et al.* 2008) we calculated a general axis of constant orientation between the North Sea region (Wadden Sea) and breeding grounds in western Siberia (237–57°, loxodrome, solid line; Figure 4). For comparison, we extrapolated the mean track direction of Dunlins migrating from Ottenby (234° ± 40%) both forward and backward (thick dashed line, Figure 4) assuming a constant compass course (loxodrome).

DISCUSSION

Mean flight directions of arctic shorebirds in the southern Baltic region were similar but not identical to the loxodrome axis (237°/57°; Figure 4) between main breeding and winter/staging areas (cf. Gudmundsson 1994, Green *et al.* 2002). Mean track directions differed significantly between the different samples from observation sites and ring recoveries in a way that demonstrated fine-scaled orientation changes when the shorebirds passed the southern Baltic region. Apparently, the shorebirds made gradual course changes to the right, by on average 12° between the easterly (Ottenby) and the most westerly study site (Björka, Figure 1). At the latter site they had a mean direction that agreed well with the mean direction towards the goal areas at the North Sea and surrounding region, as shown by the ring recoveries (Figure 3).

The differences in track directions between sites could not be explained by different wind conditions at the different sites. Taking the effect of wind into account demonstrated highly significant differences in track directions between sites independently of winds. Neither could the differences in mean track directions between sites be explained by distinct responses to specific topographical features, i.e. the birds were not following coastlines or prominent landmarks in any detailed way at the different sites, which is in accordance with Meltofte (2008). At Ottenby the shorebirds were departing at low altitude over the sea, while at Vitemölla and Björka the birds were flying at higher altitudes (on average 600 m above sea level, up to highest altitudes at 1800 m) and departing or crossing over a rather flat landscape. There were no indications that the shorebirds followed specific features on the ground. There is no reason to believe that the difference in track directions between sites was due to different methodology (radar *versus* visual observation) since both methods gave directions of high accuracy over flight distances of at least about 1 km (and often much longer) and since we found a significant difference in track directions already between the two radar sites.

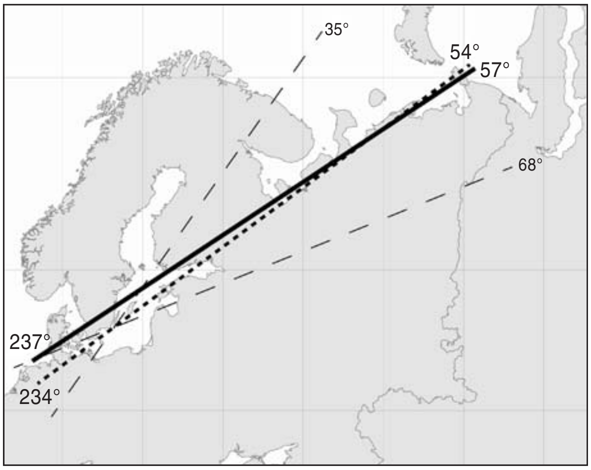

Figure 4. Map over northern Europe showing a general flight axis between the North Sea Region (Wadden Sea) and Western Siberia (237–57°, solid line). The mean track direction of Dunlins migrating from Ottenby (234°) was extrapolated both forward and backward (thick dashed line) assuming a constant compass course (loxodrome). Thin dashed lines represent 80% of the sample from Ottenby. The map is a Mercator projection.

The rightward change in orientation by on average about 12° over a longitudinal distance of only 3 degrees was almost identical to the gradual leftward course change by about 15° in the very same region by Red Knots passing in the reverse direction on spring migration as demonstrated by Gudmundsson (1994). This means that the shorebirds during autumn seemed to follow virtually the same curved routes across land and sea in the southern Baltic region as on spring migration. This similarity in routes existed in spite of the fact that migration strategies differed markedly between spring (long-distance flights in strong tailwinds) and autumn (short hop flights in opposed winds and frequent short stopover periods are common features among both juvenile and adult Dunlins on autumn migration as demonstrated by both radio telemetry and ringing data; Grönroos *et al.*, unpubl. data), suggesting that the same or similar control mechanisms determined the routes in both seasons. It is not unlikely that such similar control mechanisms apply to both Red Knots (studied during spring migration by Gudmundsson 1994) and Dunlins (dominating in this study), since both species use the same flyway between the West Siberian tundra and the North Sea region, and during autumn migration they often travel in mixed flocks (along with other arctic shorebirds in the same flyway system).

The gradual change in the orientation of shorebirds in the southern Baltic region as demonstrated in this study for the autumn migration and by Gudmundsson (1994) for the spring migration, cannot be reconciled with constant compass orientation according to any of the main compass mechanisms known to be used by migrating birds (sun-, star- or magnetic compass) as analyzed by Gudmundsson (1994). This means that we must assume that the shorebirds changed their compass courses in a rather fine-tuned way over distances of only a few hundred kilometers. This indicated that the control of flight courses and paths may be more complex than expected. It remains unknown if the birds changed their compass courses gradually or in steps and what mechanisms may operate to trigger these changes.

Why do the shorebirds make this course change along the route? If they were to follow a more direct constant geographic course from their breeding areas in West Siberia towards staging areas in the North Sea region the majority of birds would pass more to the north when passing southern Scandinavia (Figure 4). They would then have to fly longer stretches over inland areas offering fewer opportunities for stopovers. Gudmundsson (1994) suggested that the shorebirds might want to maximize the general association with coastal habitats and minimize passages across larger inland areas, thus taking a more southerly route. This possibility is supported by the findings in this study that the shorebirds used the same curved routes when passing the same region in the reverse direction during autumn as they do on spring migration. The shorebirds might travel within a slightly winding flight corridor in broad agreement with the large-scale topography, *via* the tundra coast of the Arctic Ocean, parts of the White Sea, the Gulf of Finland and the Baltic Sea to their destinations.

It is possible that social influence and learning play an important role for the development and maintenance of the shorebirds' curved flight paths in the southern Baltic region. The arctic shorebirds migrate in flocks, and the flocks are often mixed with respect to both age groups and species. Younger birds may, during their first autumn or spring migrations (perhaps mainly during the first spring migration and second autumn migration, see below), learn the general flight paths and course changes in relation to the broad-scale topography in different regions from older and experienced individuals in the flocks (as suggested already by Palmén 1874 although the birds apparently did not pinpoint specific coastlines, rivers or landmarks as assumed by Palmén). This possibility is supported by the indication that juvenile Dunlins had a significantly different (more southerly) orientation at Ottenby than adults, particularly when the juveniles travelled in flocks without any adults (Figure 2). This tendency of a more southerly orientation by juveniles is also seen from the ringing recoveries (Figure 3, Table 1). The differences in track directions between age groups could not be explained by differences in exposure to wind conditions. Taking the effect of wind into account demonstrated highly significant differences in track directions between age groups independently of winds. Our results indicate that juvenile birds to a higher degree use inland routes compared to adults which are more bound to the coasts. This pattern has also been found for Dunlins in Central and Western Europe during autumn migration where adult birds were concentrated along the coasts, whereas juveniles were observed both along the coasts and inland (Gromadzka 1989). Juveniles probably migrate on a broader front compared to adults (Meltofte 2008) and the migratory directions of juveniles in our study were more spread (Figure 2) which could explain the use of inland sites by juveniles. Also, adult birds moult their flight feathers in high-quality tidal areas like the Wadden Sea before heading for their wintering areas whereas juveniles do not moult these feathers during their first autumn which might make them less bound to coastal areas.

The possibility of learning flight paths from adults may be rather limited for juveniles on their very first autumn migration, when the juveniles migrate at a later time in the season than the adults and the overlap in timing between the age classes is not so large (Kolthoff 1896, Edelstam 1972). Also, juvenile and adult Dunlins originating from N Scandinavia and W Siberia often migrate along different routes during autumn migration. It seems like many juvenile Dunlins migrate along the Norwegian coast during their first autumn while in subsequent years they use routes more to the east through the Baltic Sea (Leslie & Lessells 1978, Tjørve & Tjørve 2007). Furthermore, juveniles and adults show no tendency of associating but rather to form segregated flocks when comparing with random age mixing in the flocks (Henningsson & Karlsson 2009). However, during their first spring migration and their second autumn migration the young birds may learn the flight path geometry in the southern Baltic Sea region more efficiently from the older generations in the flocks.

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REFERENCES

Alerstam T. 1976. Bird migration in relation to wind and topography. PhD Thesis, Lund University, Sweden.

Alerstam T. 1985. Strategies of migratory flight, illustrated by Arctic and Common terns, *Sterna paradisaea* and *Sterna hirundo*. In: Rankin M. A. (ed.) Migration: mechanisms and adaptive significance. Contributions in Marine Science 27: 580–603.

Alerstam T. 1996. The geographical scale factor in orientation of migrating birds. J. Exp. Biol. 199: 9–19.

Alerstam T. & Gudmundsson G.A. 1999. Migration patterns of tundra birds: Tracking radar observations along the Northeast Passage. Arctic 52: 346–371.

Alerstam T. & Pettersson S-G. 1991. Orientation along great circles by migrating birds using a sun compass. J. Theor. Biol. 152: 191–202.

Batschelet E. 1981. Circular statistics in biology. Academic Press, London, UK.

Edelstam C. 1972. The visible migration of birds at Ottenby, Sweden. Vår Fågelvärld, Suppl. 7.

Fransson T., Österblom H. & Hall-Karlsson S. 2008. Swedish Bird Ringing Atlas. Vol. 2. Bulls Graphics, Halmstad.

Green M. 2004. Flying with the wind – spring migration of Arctic-breeding waders and geese over South Sweden. Ardea 92: 145–160.

Green M., Alerstam T., Clausen P., Drent R. & Ebbinge B.S. 2002. Dark-bellied Brent Geese *Branta bernicla bernicla*, as recorded by satellite telemetry, do not minimize flight distance during spring migration. Ibis 144: 106–121.

Gromadzka J. 1989. Breeding and wintering areas of Dunlin migrating through southern Baltic. Ornis Scand. 20: 132–144.

Gudmundsson G.A. 1994. Spring migration of the Knot *Calidris c. canutus* over southern Scandinavia, as recorded by radar. J. Avian Biol. 25: 15–26.

Gudmundsson G.A. & Alerstam T. 1998. Optimal map projections for analysing long-distance migration routes. J. Avian Biol. 29: 597–605.

Henningsson S.S. & Karlsson H. 2009. Do adult and juvenile dunlins *Calidris alpina* form randomly mixed flocks during fall migration? J. Avian Biol. 40: 646–649.

Kolthoff G. 1896. Zur Herbstwanderung der nordischen Sumpfvögel über die Insel Öland. Festskrift för Liljeborg. Uppsala, Sweden.

Leslie R. & Lessells C.M. 1978. The migration of Dunlin Calidris alpina through northern Scandinavia. Ornis Scand. 9: 84–86.

Meltofte H. 2008. A personal view on how waders migrate using the autumn passage of Northern Dunlins as an example. Wader Study Group Bull. 115: 29–32.

Newton I. 2008. The migration ecology of birds. Academic Press, London.

Palmén J.A. 1874. Om foglarnes flyttningsvägar. German translation “Über die Zugstrassen der Vögel” published in 1876. Kejserliga Alexanders University, Finland. J.C. Frenckell, Helsinki.

Snyder J.P. 1993. Flattening the earth: two thousand years of map projections. University of Chicago Press, Chicago.

Tjørve E. & Tjørve K.M. C. 2007. Movements of Dunlins *Calidris alpina* ringed along the Norwegian coast. Wader Study Group Bull. 112: 37–44.

Wiltschko R. & Wiltschko W. 2009. Avian navigation. Auk 126: 171–743.

SAMENVATTING

Ieder najaar passeren grote aantallen steltlopers de Oostzee op weg van hun Arctische broedgebieden naar de Waddenzee. In dit artikel wordt de vliegrichting die ze daarbij aanhouden aan nader onderzoek onderworpen om te zien of deze beïnvloed wordt door de wind, topografie of leeftijd van de vogels. De auteurs hadden de beschikking over drie datasets uit zuid-Zweden: directe observaties, radar en ringgegevens. In totaal werd van bijna 800 groepen steltlopers de vliegrichting bepaald, waarbij het voornamelijk ging om Bonte Strandlopers *Calidris alpina*. De vliegrichting bleek te verschillen tussen de observatiestations: de vogels leken een flauwe bocht te maken tussen de meest oostelijke en westelijke stations. Waarom ze dit doen was niet duidelijk. Het gedrag kon in ieder geval niet verklaard worden door verschillen in windrichting, of door opvallende landschapskenmerken (zoals de kustlijn). Er werd ook een verschil in vliegrichting gevonden tussen adulte en juveniele vogels. Jonge vogels passeerden zuid-Zweden in een breed front, terwijl adulten geconcentreerd langs de kust vlogen. Omdat juvenielen de reis voor het eerst maken en over het algemeen niet met de volwassen vogels mee vliegen, moeten ze waarschijnlijk nog leren hoe de beste richting aan te houden.

(KK)

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