

A polar system of intercontinental bird migration

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Studies of bird migration in the Beringia region of Alaska and eastern Siberia are of special interest for revealing the importance of bird migration between Eurasia and North America, for evaluating orientation principles used by the birds at polar latitudes and for understanding the evolutionary implications of intercontinental migratory connectivity among birds as well as their parasites. We used tracking radar placed onboard the ice-breaker Oden to register bird migratory flights from 30 July to 19 August 2005 and we encountered extensive bird migration in the whole Beringia range from latitude 64° N in Bering Strait up to latitude 75° N far north of Wrangel Island, with eastward flights making up 79% of all track directions.

The results from Beringia were used in combination with radar studies from the Arctic Ocean north of Siberia and in the Beaufort Sea to make a reconstruction of a major Siberian–American bird migration system in a wide Arctic sector between longitudes 110° E and 130° W, spanning one-third of the entire circumpolar circle. This system was estimated to involve more than 2 million birds, mainly shorebirds, terns and skuas, flying across the Arctic Ocean at mean altitudes exceeding 1 km (maximum altitudes 3–5 km). Great circle orientation provided a significantly better fit with observed flight directions at 20 different sites and areas than constant geographical compass orientation. The long flights over the sea spanned 40–80 degrees of longitude, corresponding to distances and durations of 1400–2600 km and 26–48 hours, respectively. The birds continued from this eastward migration system over the Arctic Ocean into several different flyway systems at the American continents and the Pacific Ocean. Minimization of distances between tundra breeding sectors and northerly stopover sites, in combination with the Beringia glacial refugium and colonization history, seemed to be important for the evolution of this major polar bird migration system.

Keywords: bird migration; Arctic birds; Arctic Ocean; migratory connectivity; great circle orientation

1. INTRODUCTION

In spite of long-lasting exploration and charting of the Arctic during five centuries, often by adventurous, strenuous and tragic expeditions (Hayes 2003), the knowledge about bird migration routes remains limited (Johnson & Herter 1990) and major systems of migratory connectivity (Webster *et al.* 2002) in the Arctic region may still await discovery. Improved knowledge of bird migration in the Arctic is important for understanding how bird distributions have changed with glacial history and will be affected by climate change, how bird-borne pathogens like avian influenza may connect across polar sectors (Olsen *et al.* 2006) and for understanding the orientation principles used in migration under the special celestial and geomagnetic conditions that prevail at polar latitudes (Alerstam *et al.* 2001).

We have earlier used tracking radar onboard ice-breaking ships to chart bird migration patterns in the Arctic Ocean along both the Northeast and Northwest Passages (Alerstam & Gudmundsson 1999a; Gudmundsson *et al.* 2002). During these studies, we discovered intensive high-altitude eastbound migration by mainly shorebirds, skuas and terns in July and August over the Arctic Ocean north of

the Siberian tundra coast in a wide sector including the Laptev and East Siberian Seas between longitudes 110 and 170° E (Alerstam & Gudmundsson 1999a). The birds' flight directions suggested that these movements formed part of a major postbreeding migration system that was not restricted to flights across the Arctic Ocean between central and eastern Siberia, but probably also involved long flights between Siberia and North America (Alerstam & Gudmundsson 1999b). Our studies in the Beaufort Sea (at longitudes 130–140° W) revealed similarly intensive eastbound movements of birds arriving from northern Alaska and possibly also directly from Siberia across the Arctic Ocean (Gudmundsson *et al.* 2002). The flight directions north of Siberia as well as in the Beaufort Sea suggested that the birds were not maintaining constant geographical courses but changed their directions in approximate accordance with great circle orientation, possibly through sun compass orientation without correction for the longitude-dependent shift in local time (Alerstam *et al.* 2001).

The aim of the present study was to explore the postbreeding bird migration pattern in July/August in the Beringia sector of the Arctic Ocean to fill the crucial gap between longitudes 170° E and 140° W which remained from our earlier studies. For this purpose, we placed two tracking radar stations onboard the ice-breaker Oden to

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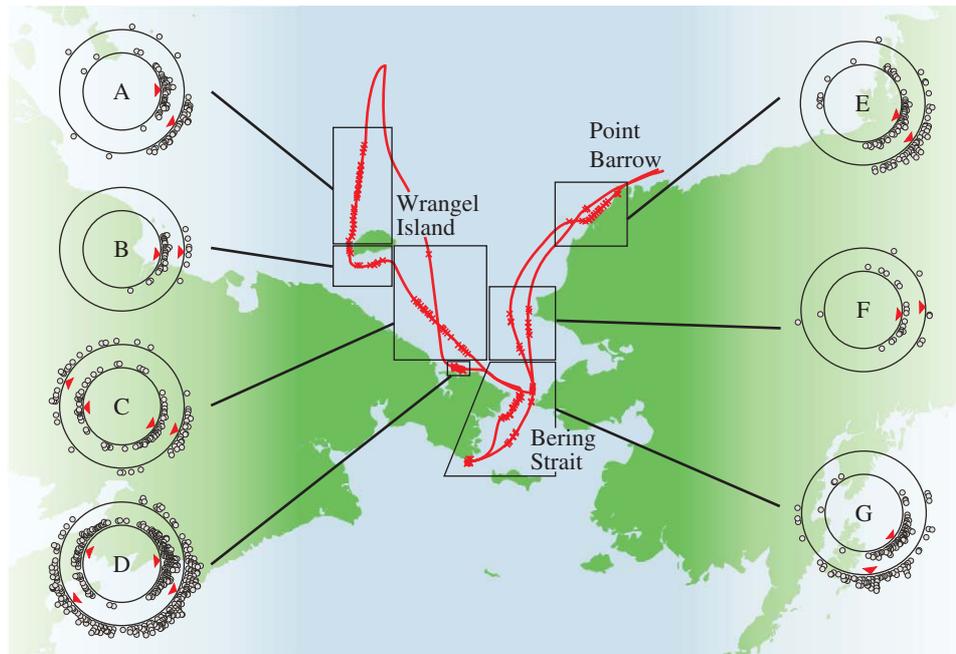


Figure 1. Track and heading directions of migrating birds recorded by radar from the ice-breaker Oden from 30 July to 19 August 2005. The route of Oden is shown on the map (entering and leaving the Beringia region at Point Barrow), with crosses indicating positions where bird tracking data were obtained (often overlapping). The map is a stereographical polar projection. Track (inner circles) and heading (outer circles) directions are plotted in circular diagrams for the seven areas indicated on the map. Grey dots show directions of single radar tracks, and mean directions (calculated as mean vectors) are shown by red arrowheads. For bimodal circular distributions, mean directions were calculated separately for eastward and westward migrations (tracks in the eastern and western semicircle, respectively). Detailed results about numbers, altitudes and directions of radar tracks for the seven areas are given in table 1.

monitor bird migration patterns during the expedition Beringia 2005 (Swedish Polar Research Secretariat 2006). Our results from the Beringia sector, as presented below, allow us to draw firm conclusions about the bird migration links between the Eurasian and North American continents. Furthermore, when combined with the results from the two earlier expeditions, we will obtain a more complete picture of the bird migration system in a wide Arctic sector between 110° E and 130° W, spanning one-third of the entire circumpolar circle. This synthesis will include reconstruction of the geographical extent of the migratory system with orientation, distances, durations and altitudes of flights across the Arctic Ocean. In addition, we will discuss this migration system in an evolutionary perspective, with its implications for the exchange of birds and parasites between continents.

2. MATERIAL AND METHODS

Flights of migrating birds were measured by tracking radar from the ice-breaker Oden from 30 July to 19 August 2005 during the Swedish research expedition Beringia 2005 (Swedish Polar Research Secretariat 2006). Methods were similar to those used on earlier expeditions to the Arctic Ocean (Alerstam & Gudmundsson 1999*a,b*; Gudmundsson *et al.* 2002). We recorded both single birds and flocks of birds, usually at a distance of 3–10 km from the ship. Our observations were made between longitudes 177° E and 157° W and latitudes 64° and 75° N (figure 1).

We used two tracking radars to collect all bird movements: 'PV882' (X-band, 200 kW peak power, 1.5° beam width, pulse duration $0.25 \mu\text{s}$, maximum tracking error 0.06° and 10 m in position) and 'PV301' (X-band, 200 kW peak power, 1.65° beam width, pulse duration of $0.5 \mu\text{s}$ and maximum

tracking error approx. 50 m in position). These two radar types are very similar in construction and performance, with the principle of operation being the same and most of the internal electronics identical. The radars were placed one on each side of the ship, 20 m above sea level, each covering approximately 240° of the horizon with some overlap. Both the radars were used to collect data, but usually not at the same time owing to RF interference between our radars and the ship radar system. The radars were operated with manual antenna control until an aerial target was discovered. When the radar had been locked at the target, operation of the radar was switched to automatic tracking mode. Datasets of distance, elevation and azimuth were collected until the radar lost the target or tracking was cancelled by the operator. Datasets were recorded by a computer every 1 or 2 s, depending on which radar we were operating.

To measure the atmospheric wind at higher altitudes and calculate true heading and air speed of the target, we released helium-filled balloons with a reflector every second or third hour and tracked them for as long time as possible.

We could not use the radars when the ship was breaking ice, and tracks were collected when the ice-breaker was cruising through a very scattered pack ice or open water (approx. 65% of the tracks) or was stationary. To adjust for the ship's orientation and movement, we collected real-time data every 5 s from the navigation system about heading, course over ground, speed over ground, geographical position, wind speed and wind direction near the ship's top level (30 m above sea level).

All recordings from radar and ship, path calculations and data compilation were performed with customized software developed in DELPHI v. 7 (Borland International, Inc., CA, USA).

Table 1. Flight altitudes and directions of migrating birds as recorded by tracking radar in the Beringia region from 30 July to 19 August 2005. (Altitudes are in metres above sea level with standard deviations (s.d.) in parentheses. Mean vector directions are given with mean vector lengths (r) within parentheses. Area C and D with bimodal directional distributions (figure 1) are also presented with datasets subdivided in east/west groups based on track directions. Mean altitudes and track directions are based on the total number of observations, while mean heading directions are based on the number of tracks given in parenthesis (cf. figure 1).)

area	number of observations	altitude		direction	
		mean	maximum	track	heading
A	49 (44)	1267 (746)	3569	88° (0.84)	122° (0.81)
B	32 (7)	1468 (962)	3442	99° (0.92)	93° (0.97)
C	67 (52)	849 (640)	2961	163° (0.27)	116° (0.15)
C—west	29 (27)	570 (177)	1075	268° (0.76)	292° (0.60)
C—east	38 (25)	1062 (774)	2961	121° (0.84)	113° (0.97)
D	252 (237)	850 (594)	3844	71° (0.44)	147° (0.51)
D—west	73 (71)	705 (498)	2245	290° (0.81)	235° (0.86)
D—east	179 (166)	910 (621)	3844	85° (0.91)	120° (0.81)
E	61 (52)	2029 (965)	4578	111° (0.62)	127° (0.88)
F	19 (7)	1625 (235)	3743	97° (0.69)	89° (0.58)
G	77 (75)	1550 (919)	4023	129° (0.81)	171° (0.82)
all	557 (474)	1175 (855)	4578	98° (0.51)	143° (0.56)

Before the final analysis, we removed all tracks with irregular paths and with extensive gaps in the tracking record (because the radar was temporarily off the target). We also removed tracks that lasted for less than 20 s. The position data from five or ten successive recordings (depending on sampling intervals of 1 or 2 s) were averaged into a 10 s mean position and the resulting intervals were used to calculate mean speed over ground and track direction (ground speed vector) of the target. The speed vector of the ship was added to the data (ground speed vector of the target) to compensate for the ship's movement. Furthermore, heading direction and air speed of the target (air speed vector) was calculated by subtracting the wind vector at the altitude where the target was flying (wind data were available for 474 of the 557 tracks).

Data were transferred to MATLAB v. 5.2 (The MathWorks Inc., MA, USA) for the final calculations of sample mean directions, mean vector lengths and circular statistics, according to Batschelet (1981).

3. RESULTS AND DISCUSSION

(a) Migration pattern in the Beringia sector

We recorded a total of 557 radar tracks of migrating birds during 203 hours of radar operation at seven different areas of the Beringia region (figure 1; table 1). The majority of the radar echoes tracked were of flocks of birds, but a minority referred to birds flying solitarily, as judged from the radar echo signatures. Tracks lasted between 20 and 604 s, with a mean tracking time of 138 s. Both track directions (re-ground) and heading directions (re-air) are presented in figure 1 and table 1.

Bird migration was recorded over the whole range of the Beringia sector from latitude 64° N in the Bering Strait up to 75° N far north of Wrangel Island. Migration was mainly eastbound with 79% of the track directions falling in the eastern semicircle. Westerly migration was encountered on some occasions, on 6–9 August (area D) and 15/16 August (area C), taking place simultaneously with the main easterly migratory flow. The westerly migrants were flying at lower altitudes than the eastbound birds and over the Chukchi Sea (area C); many of them were

night-migrating passerines as indicated by their characteristic radar echo signatures as well as relatively low airspeeds approximately 10 m s⁻¹. Mean airspeed of birds in the eastward migration was 14.1 m s⁻¹ (s.d. 3.6 m s⁻¹, $n=367$; further details about radar and field observations in Hedenström *et al.* in preparation).

The overall mean track direction was close to east, while mean heading direction, owing to dominating winds from the southwesterly and southeasterly quadrants, was towards southeast. Altitudes were often very high with mean levels exceeding 1 km and maximum levels reaching above 3 or even 4 km, particularly at and north of Wrangel Island and off the coast of Northwest and West Alaska.

Our results demonstrate a major flow of eastward high-altitude migration close to the Siberian coast but also far offshore over the open Arctic Ocean with birds arriving at Northwest and West Alaska and the Bering Strait after long transoceanic flights from Siberia. The tracks off Northwest Alaska and Point Barrow (showing the highest altitudes in our sample; table 1) are likely to reflect incoming migrants after flights that have passed far north of Wrangel Island, in good agreement with our records from area A, and indicating the possibility of flights passing even north of area A. Migrants over Bering Strait (area G) showed more southeasterly and southerly tracks and headings, respectively, indicating that the migrants, although still at high altitudes, have veered towards Southwest Alaska and the eastern Bering Sea, presumably under topographic influence.

Flocks of shorebirds, skuas and terns are most likely to make up this major eastbound migration system (Alerstam & Gudmundsson 1999a; Gudmundsson *et al.* 2002; Hedenström *et al.* in preparation). Our results fully confirm earlier fragmentary radar observations of high-altitude (reaching near 3 km above sea level) eastward migration at the northern Alaska coast and arriving at Northwest and West Alaska in July and August (Flock 1972, 1973). Flying too high to be recorded by visual field observations, it was conjectured that these migrants were shorebirds, which was also assumed for the reverse spring (May and June) pattern of extensive broad-front

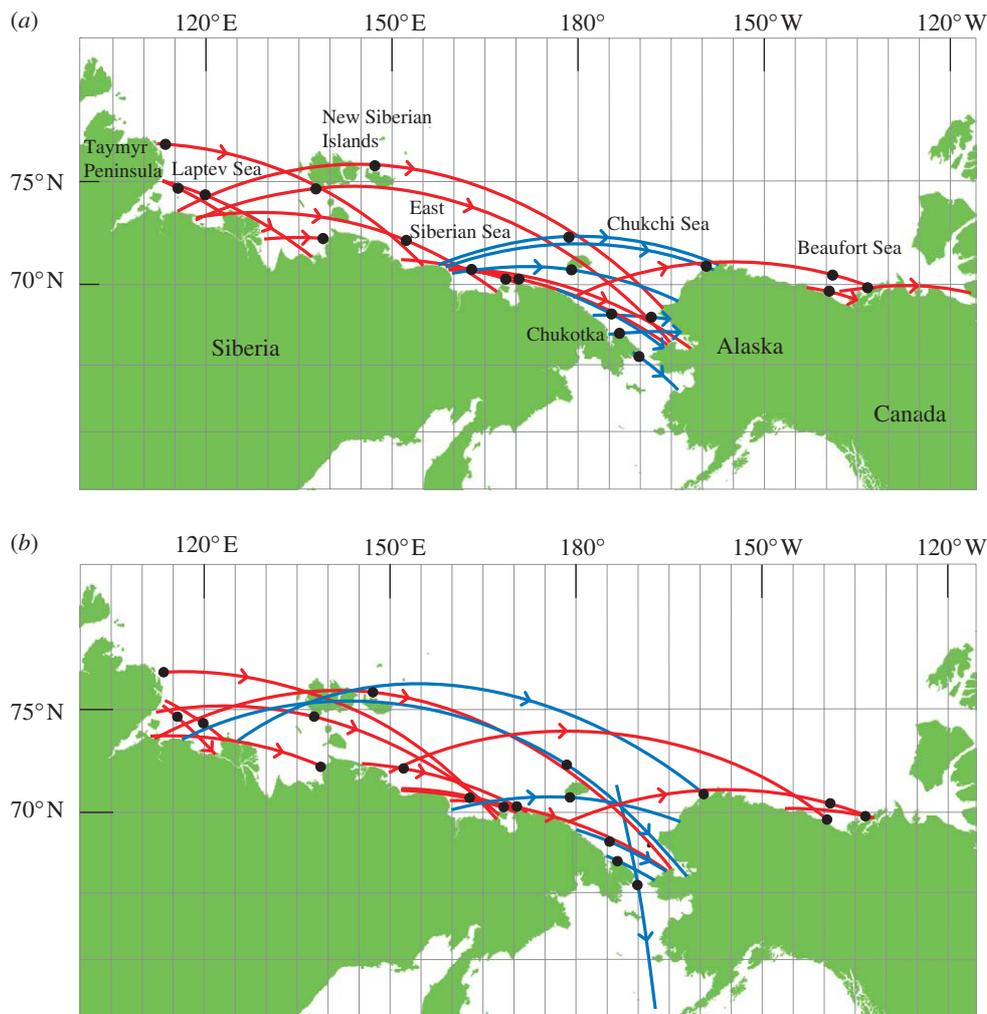


Figure 2. Mean track and heading directions of eastward bird migration in July/August over the Arctic Ocean extrapolated as great circle routes on Mercator map projections. (a) Map showing extrapolations based on mean track directions (20 sites) and (b) map based on mean heading directions (19 sites; area F west of Alaska excluded because of non-significant mean heading direction; see table 1). Radar data were available from sites or areas indicated by black dots, based on studies along the Northeast Passage in Siberia (Alerstam & Gudmundsson 1999a), in the Beaufort Sea (Gudmundsson *et al.* 2002) and in the Beringia region (present study). Routes extrapolated from Beringia data are shown in blue. Extrapolations of constant geographical compass directions (not shown), which would have appeared as straight lines on this map projection, show significantly worse fit than great circle routes (see text).

and high-altitude westward flights at the Beaufort Sea (Flock 1972, 1973; Richardson & Johnson 1981).

(b) Reconstruction of a polar Siberian–American migration system

(i) Geographical extent, flight routes and orientation

We plotted and extrapolated mean track and heading directions of eastward migration over the Arctic Ocean, based on the samples of radar tracks obtained at 20 different sites and areas between longitudes 110° E and 130° W during the three expeditions to Siberia, Beaufort Sea and Beringia, respectively (trajectories assuming great circle orientation plotted on Mercator projections in figure 2).

The observed directions strongly indicated that the birds changed their courses in a clockwise fashion during their flights across the Arctic Ocean, in approximate accordance with great circle orientation. This is illustrated by the fact that extrapolations based on the assumption of constant geographical compass orientation often produced obviously invalid trajectories (arriving from the Arctic Ocean north of Taymyr Peninsula or pointing

towards the Canadian high Arctic Archipelago and Greenland). Out of the 20 mean track directions at different sites, constant course extrapolations produced eight such invalid cases, while there were no invalid cases among the great circle extrapolations (figure 2a). Similarly, mean heading directions were available from 19 sites, showing invalid extrapolated constant course trajectories in eight cases but only one case of invalid great circle trajectory (figure 2b). Thus, great circle orientation provides a significantly better fit with observed flight directions than constant geographical compass orientation ($p=0.003$ and 0.021 for track and heading directions, respectively; Fisher's exact probability two-tailed tests). The invalid great circle trajectory (arriving from the central Arctic Ocean, cf. figure 2b) is associated with a southerly mean heading at Bering Strait, which is probably explained by topographical responses in this special area (see above). This analysis provides further support for the great circle orientation of Arctic birds (Alerstam & Pettersson 1991; Alerstam & Gudmundsson 1999a,b; Alerstam *et al.* 2001).

The similarity in general pattern between extrapolations based on track and heading directions, respectively (figure 2), shows that both track and heading directions change in a consistent way in spite of wind drift effects (cf. Green *et al.* 2004). Whether actual flight paths are best reflected by track or heading directions depends on the variability of winds along the routes. Since wind conditions have differed considerably between different flights, we expect that actual flight paths show elements from extrapolations based on both track and heading directions, which together form a coherent pattern of possible flight routes across the Arctic Ocean (figure 2).

The system of eastward migration was recorded up to latitudes 74–77° N off Taymyr Peninsula, north of the New Siberian Islands and north of Wrangel Island, corresponding to a broad corridor extending from the coast of the Siberian mainland and 300–560 km northwards over the Arctic Ocean and its islands.

(ii) Distances, durations and altitudes of flights

Both track and heading directions suggested that migrants arrived in Alaska besides from eastern Siberia also by direct flights from tundra areas as far west as the Laptev Sea region, west of the New Siberian Islands. Also direct flights from Siberia into the Beaufort Sea and to Northwest Canada were supported by the observed flight directions (figure 2). The long flights in the eastward migration system are likely to span over 40–80 degrees of longitude corresponding to distances of 1400–2600 km across the Arctic Ocean (figure 2). With mean ground speeds varying between 11 and 23 m s⁻¹ (overall average approx. 15 m s⁻¹; Alerstam & Gudmundsson 1999a; Gudmundsson *et al.* 2002; Hedenström *et al.* in preparation), the duration of these long flights falls in the interval of 17–66 hours, typically 26–48 hours. High flight altitudes, reaching 2–5 km above sea level, were characteristic throughout the range of the eastward migration system (figure 3).

(iii) Magnitude of migration

Our tracking radar studies can be used to provide only a very rough estimate of the minimum number of migrating birds involved, since we sampled only a small minority of the flocks or individuals passing within the radar range. The number of radar echoes of eastbound bird flocks tracked per hour of radar operation varied between 2.2 and 4.3 for the radar studies at Siberia, Beaufort and Beringia, with an overall mean of 3.1. The fact that we operated the radar mostly during times of migratory activity will lead to an overestimation of the true traffic rate; but considering the high regularity of migration (samples were obtained from almost all sites that were visited even if only during as short periods as single days), this bias was probably vastly less important than the effect of underestimation because only a small proportion of the echoes were sampled for tracking. We believe that the true mean traffic rate must have been at least four times the estimate based on tracked echoes. We derived the minimum factor of 4 from two components of underestimation. Firstly, effective search time was only about half of the total radar operation time when taking into account the time of tracking birds and helium balloons. Secondly, on most radar search occasions, it was obvious that there was at least one additional simultaneous target,

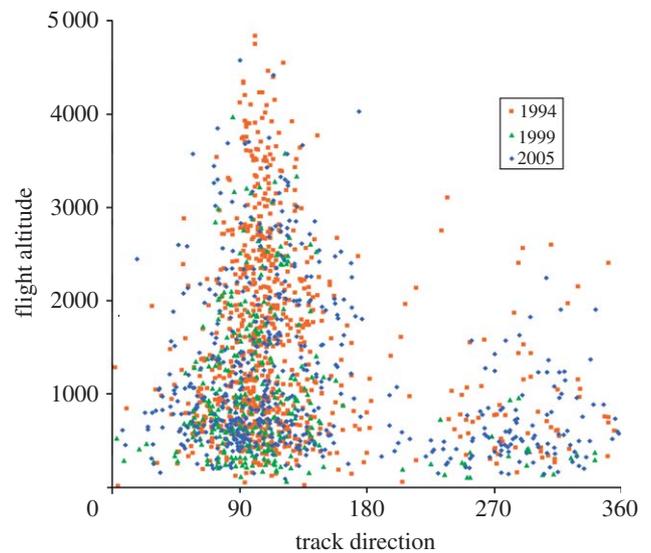


Figure 3. Flight altitudes (m above sea level) in relation to track direction for the total sample of radar tracks recorded during July/August over the Arctic Ocean east of Taymyr Peninsula (longitudes 113–171° E) in 1994, in the Beaufort Sea (longitudes 133–140° W) 1999 and in the Beringia region (longitudes 177° E–157° W) 2005 (present study). Eastward migration often reaching very high altitudes was a dominating feature throughout the combined study range from longitudes 110° E to 130° W.

besides the target tracked, and on some occasions there were several tens of targets of migrating bird flocks simultaneously within radar range. Hence, the factor 4 must be regarded as a very conservative estimate. This factor gives a mean traffic rate of 12 flocks h⁻¹ across a frontal width of approximately 15 km at the radar station. Applying this estimate across a total frontal width of at least 450 km and a total time period of at least 50 days (radar records are from the period 4 July–19 August) gives a total minimum of 0.4 million migrating flocks. With a mean flock size of at least 5 (cf. Alerstam & Gudmundsson 1999a), the entire system of eastward migration over the Arctic Ocean is likely to involve no less than 2 million birds, and possibly considerably more.

(iv) Species involved

The large-scale eastward migration over the Arctic Ocean is linked to several major flyways at the American continents and the Pacific Ocean (Morrison 1984; Gill *et al.* 1994; Morrison *et al.* 2001).

- (i) The Eastern flyway is used by species such as semi-palmated sandpiper *Calidris pusilla*, white-rumped sandpiper *Calidris fuscicollis*, pectoral sandpiper *Calidris melanotos* and American golden plover *Pluvialis dominicus* that migrate across the top of North America towards Hudson Bay and further across the West Atlantic Ocean towards South America (Atlantic side). The breeding ranges of most of these species (for information about breeding distributions of different species see American Ornithologists' Union (1992–2002) and del Hoyo *et al.* (1996)) do not extend further west than northern and western Alaska, which makes it probable that most of these species fly over the Arctic Ocean only in the Beaufort Sea region.

However, the pectoral sandpiper has a breeding range extending far westwards into Siberia (even beyond 110° E) and this species may thus participate in the transoceanic flights across the Arctic Ocean throughout the full range of this migration system (figure 2).

- (ii) Some Arctic shorebirds participating in the eastward migration across the Beaufort Sea may veer more southwards at the Mackenzie basin to follow the Interior flyway across the North American continent towards the Gulf of Mexico and into South America. Baird's sandpiper *Calidris bairdii* with a breeding range extending as far west as Chukotka and Wrangel Island, belongs to this group of species.
- (iii) A large number of species use the East Pacific flyway, involving both pelagic birds like red phalarope *Phalaropus fulicarius*, Arctic tern *Sterna paradisaea* and pomarine skua *Stercorarius pomarinus* which travel across the Beringia region into the eastern Pacific Ocean to continue south off the South American coast, and coastal birds like long-billed dowitcher *Limnodromus scolopaceus*, western sandpiper *Calidris mauri*, dunlin *Calidris alpina* and grey plover *Pluvialis squatarola*, which after crossing the Beringia region follow the west coasts of the American continents. Some of these species have breeding ranges extending from Alaska far westwards along the Siberian tundra coast. The red phalarope is an abundant species that figures prominently in our field observations (Hedenström *et al.* in preparation) and is known to concentrate in late summer at ice edges far out in the Beaufort Sea north of Alaska (Johnson & Herter 1990), thus probably being a particularly important member of the migration system over the Arctic Ocean. One cannot exclude that some Arctic terns and red phalaropes, after travelling eastwards into the Beaufort Sea, embark on a long high-altitude flight step overland across western North America to reach the Pacific Ocean off Mexico (Villasenor & Phillips 1994; Alerstam & Gudmundsson 1999a).
- (iv) Other shorebird species travel first eastward to Alaska, where they store large fuel reserves before continuing on more southerly courses by long transoceanic flights across the central Pacific Ocean to winter quarters in Oceania, New Zealand and Australia. Turnstone *Arenaria interpres*, Pacific golden plover *Pluvialis fulva* and juvenile sharp-tailed sandpiper *Calidris accuminata* belong to this category (Thompson 1974; cf. Gill *et al.* 2005, about trans-Pacific flights also by shorebirds breeding in Alaska).

We conclude that the Siberian–American system of eastward bird migration across the Arctic Ocean in July and August involve mainly shorebirds, terns and skuas. Some populations of, for example, red phalarope, pectoral sandpiper and Arctic tern may travel eastward in this system all the way from the Laptev Sea to the Beaufort Sea region, while other populations and species participate in the eastward migration only within more restricted sectors. The birds exit this system into several different flyways, leaving the Beringia region towards winter

quarters at the eastern and western coasts of the American continents and in the Pacific Ocean including Oceania, New Zealand and Australia.

(c) *Evolution of the Siberian–American migration system*

Why do birds travel far offshore over the Arctic Ocean when their winter destinations are at southerly latitudes, often in the Southern Hemisphere?

One important explanation is that they follow close to the great circle routes associated with initial departure directions towards east (ENE–ESE) across the Arctic Ocean for birds travelling from northern Siberia or Alaska to South America and the eastern Pacific Ocean (Alerstam & Gudmundsson 1999a,b).

This migration system may also be influenced by the historical situation during the last glacial maximum (approx. 18 000 years BP) when Beringia was a tundra land bridge between Asia and North America, extending over vast exposed continental shelf areas and surrounded by huge inland glaciers in North America (the Laurentide and Cordilleran ice sheets) and western Siberia/northern Europe (Frenzel *et al.* 1992; Kraaijeveld & Nieboer 2000). The large American ice sheets probably prevented bird migration between Beringia and the eastern and interior parts of the North American continent. Species breeding on the North American tundra south of the large ice sheets have probably expanded into Alaska with the retreat of these ice sheets, establishing the link between Beringia and the Eastern and Interior flyways during Late Pleistocene (10 000–13 000 years BP). That southern periglacial refugia have been an important source for the postglacial colonization of arctic North America is indicated by molecular evidence from true lemmings (Fedorov *et al.* 2003), making it probable that these refugia have been important for migrant tundra birds as well, with some of these bird species extending their postglacial colonization of North America into Beringia and beyond.

The Bering Land Bridge and western Alaska were to a large degree covered by mesic tundra (Elias *et al.* 1996; S. Elias 2007, personal communication) probably providing not only ample breeding resources for migratory tundra birds but also resources allowing extensive fuel deposition in preparation for long flights towards the west coast of North America and the Pacific Ocean. Thus, eastward postbreeding migration from Siberia to Beringia and further into the East Pacific flyway and across the central Pacific Ocean may have existed also during the last glacial maximum. A limited amount of south–westward postbreeding migration into Beringia from small refugia in the Canadian Arctic northwest of the main ice sheet may also have existed during the last glacial maximum (the biological significance of these refugia is supported by molecular data for collared lemmings; Fedorov & Stenseth 2002).

Tundra persisted along the arctic coast of Siberia and on its Arctic islands throughout the following Holocene climatic optimum (approx. 8000 years BP), although in a reduced extent owing to the northward advance of the boreal forest during this period (Kraaijeveld & Nieboer 2000; S. Elias 2007, personal communication). Thus, the eastward postbreeding migration from Siberia towards Beringia probably persisted during this warm period even if numbers of tundra migrants were reduced.

Why is westward migration across the Arctic Ocean at Alaska and eastern Siberia of such small magnitude compared with the major eastward flow of migrants? One group of westbound migrants in the Beringia region consisted of nocturnal passerine migrants, encountered during our radar studies mainly over the Chukchi Sea (area C, figure 1). This group consists of species like arctic warbler *Phylloscopus borealis*, yellow wagtail *Motacilla flava*, northern wheatear *Oenanthe oenanthe* and bluethroat *Luscinia svecica* (Lehman 2005), which have colonized western Alaska from the Old World while maintaining their winter quarters in southern Asia and eastern Africa (wheatear). Another group of westbound migrants were ducks and geese on moult migration (Johnson & Richardson 1982; Hedenström *et al.* in preparation) probably travelling mainly at low altitudes close to the coastline (cf. area D in figure 1), where also gulls may have been involved in the westerly movements.

There seems to be only one good example of a shorebird species that have colonized the eastern Siberian tundra from the west maintaining its westward postbreeding migration towards winter quarters in southern Asia and in Africa, and that is the ruff *Philomachus pugnax*. Westbound flights recorded by radar at and south of the New Siberian Islands were possibly due to this westward migration of ruff (Alerstam & Gudmundsson 1999a).

There is a distinct migratory divide at the Taymyr Peninsula, about longitudes 100–110° E, with westward migration across the Arctic Ocean dominating to the west of this divide (Alerstam & Gudmundsson 1999a). Many of the migrants involved in these westerly movements, including shorebirds, terns and skuas, continue from the tundra of western Siberia and northern Russia into the East Atlantic flyway along the coasts of Europe and Africa. Species that have colonized western Siberia and northern Russia from eastern Siberia after the last glacial maximum must therefore have changed their postbreeding migration towards west, an evolutionary process that has possibly been facilitated by the overlap with species colonizing the same areas from the west and south.

Why do not more birds from eastern Siberia and Beringia, besides the ruff, migrate westwards to join the East Atlantic flyway? A possible explanation is the much longer flights across the Arctic Ocean that this would entail compared with eastward migration to enter the American and Pacific flyways. The evolution of the migration patterns of Arctic shorebirds seemed to be constrained not so much by total migration distances as by travel distances across the Arctic Ocean, showing a distinct avoidance of migration across the central parts of the Arctic Ocean (Henningsson & Alerstam 2005a). Minimization of distances between the tundra breeding sectors and the northerly stopover sites, where birds exit or enter the major flyway systems, seems to be an important selection criterion for the evolution of shorebird migration in the Arctic region (Henningsson & Alerstam 2005a,b). Hence, the migratory divide at Taymyr coincides with the mean position between the Northwest European stopover sites associated with the East Atlantic flyway and the Alaskan stopover sites connected to the Pacific and American flyways. Long transpolar flights across the central Arctic Ocean are associated with enhanced costs and risks, and possibly also orientation difficulties, compared with shortcut flights across the peripheral parts

of the Arctic Ocean (Alerstam *et al.* 1986; Gudmundsson & Alerstam 1998; Henningsson & Alerstam 2005a).

In view of the extensive intercontinental Siberian–American migration system across the Arctic Ocean, as demonstrated in this study, it is surprising that avian influenza viruses seem to divide into two rather well-defined Eurasian and American lineages (Olsen *et al.* 2006). However, the phylogenetic relationships may be quite different if viruses from arctic birds were considered to a larger degree, as indicated by findings of viruses with gene segments of both Eurasian and American avian origins among shorebirds and auks (Makarova *et al.* 1999; Wallensten *et al.* 2005).

The polar migration system involving millions of birds travelling at high latitudes across thousands of kilometres of the Arctic Ocean has a profound importance for the Eurasian–American intercontinental migratory connectivity (Webster *et al.* 2002) of birds as well as their parasites.

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