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Migration Patterns of Tundra Birds: Tracking Radar Observations along the Northeast Passage

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ABSTRACT. Bird migration was recorded by tracking radar and visual observations at 15 study sites, situated between 50˚E and 170˚E along the Northeast Passage, during a ship-based expedition in July and August 1994. A total of 1087 radar tracks (average duration 220 s) of bird flocks on postbreeding migration were recorded. Migration was dominated by waders and to a certain degree also skuas (especially pomarine skua *Stercorarius pomarinus*). Terns, gulls, ducks, and geese were also among the migrants tracked by radar. The radar data revealed a major migratory divide at about 100˚E (Taymyr Peninsula), with mainly eastbound migration to the east of this divide, and mainly westbound migration to the west of it. The main stream of eastbound migration was directed toward the sector 90–120˚ and that of westbound migration toward the sector 240–270˚; these directions are broadly in parallel with the coasts of the Arctic Ocean east and west of the Taymyr Peninsula, respectively. There was also important ENE migration, which provided strong indications of long-distance flights along orthodrome-like routes directly between Siberia and North America, across vast expanses of the Arctic Ocean pack ice. Analysis of flight directions in relation to wind indicated complete compensation for wind drift. Mean flight altitude was 1.3 km, and the birds regularly travelled at high altitudes above 3 km (9% of the tracks) up to a maximum height of 4.8 km. They preferred to migrate on occasions and at altitudes with following winds; such conditions provided an average gain in speed of 4.6 m/s. There were also recurrent cases of birds migrating in tailwinds of gale force, between 18 and 24 m/s. The birds' airspeed varied between 8 and 22 m/s, with a mean of 14 m/s. Airspeed was significantly correlated with altitude, wind, and vertical speed and seemed to be intermediate between the speeds for minimum power and maximum range predicted by aerodynamic theory.

Key words: Arctic Ocean, bird flight, bird migration, Northeast Passage, orientation, radar, Siberia

RÉSUMÉ. Durant une expédition ayant pour base un navire, réalisée en juillet et août 1994, on a enregistré la migration des oiseaux à l'aide d'un radar de poursuite et d'observations visuelles dans 15 zones d'étude situées entre 50 et 170˚ de longit. E., le long du passage du Nord-Ouest. On a enregistré un total de 1087 poursuites radar (d'une durée moyenne de 220 s) de volées d'oiseaux en migration après la nidification. La migration était dominée par les échassiers et, à un certain degré également, par les labbes (en particulier le labbe pomarin *Stercorarius pomarinus*). Les sternes, goélands, canards et oies étaient aussi au nombre des migrants suivis au radar. Les données de radar révèlent une scission migratoire majeure à environ 100˚ de longit. E. (presqu'île de Taïmyr), avec surtout une migration vers l'est, à l'est de cette division, et une migration vers l'ouest, à l'ouest de cette division. Le courant principal de la migration en direction de l'est était dirigé vers le secteur allant de 90 à 120˚ et celui de la migration en direction de l'ouest, vers le secteur allant de 240 à 270˚; ces directions sont en gros parallèles aux rivages de l'océan Arctique à l'est et à l'ouest de la presqu'île de Taïmyr respectivement. Il y avait aussi une importante migration E.-N.-E., qui offrait une indication assez précise de vols de longue distance suivant un tracé ressemblant à la ligne orthodromique directe entre la Sibérie et l'Amérique du Nord, au travers de vastes étendues de la banquise de l'océan Arctique. L'analyse des directions de vol par rapport aux vents révèle une compensation totale pour la dérive due au vent. L'altitude moyenne de vol était de 1,3 km, et les oiseaux voyageaient régulièrement à altitude élevée, allant de 3 km (pour 9 p. cent des poursuites) à une hauteur maximale de 4,8 km. Les oiseaux préféraient parfois effectuer leur migration à haute altitude avec des vents arrière, de telles conditions offrant un gain de vitesse moyen de 4,6 m/s. On a observé des cas répétés d'oiseaux qui migraient avec un vent arrière soufflant en tempête, entre 18 et 24 m/s. La vitesse relative des oiseaux variait entre 8 et 22 m/s, avec une moyenne de 14 m/s. Cette vitesse relative était corrélée fortement avec l'altitude, le vent et la vitesse verticale, et semblait être intermédiaire entre les vitesses prédites par la théorie aérodynamique pour la puissance minimale et la portée maximale.

Mots clés: océan Arctique, vol d'oiseau, migration d'oiseaux, passage du Nord-Est, orientation, radar, Sibérie.

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INTRODUCTION

A multitude of migratory birds travel to breed during the short arctic summer on the tundra, with its vast wetlands and thawing soils on top of the permafrost. Many of the shorebirds, skuas, and terns depart from the tundra by July and August and make astounding global migration journeys to winter quarters in the Southern Hemisphere.

The migration patterns and flight performance of arctic birds have aroused fascination ever since the first polar voyages and expeditions. The numerous field studies and extensive literature on this topic are reviewed by Johnson and Herter (1990) and Vaughan (1992). While visual field observations are fundamental for knowledge of bird migration patterns, radar permits the registration of bird migration beyond the range of vision—at high altitudes, above fog and clouds, and in poor light and darkness. Furthermore, radar allows precise measurements of altitudes (obtainable with tracking radar but not surveillance radar), speeds, and directions. Radar studies have been conducted at only a few Arctic sites: in Alaska, along the Beaufort Sea coast of Canada, in Greenland, in Iceland, and in the central Arctic Ocean (Flock, 1972, 1973; Richardson and Johnson, 1981; Johnson and Richardson, 1982; Alerstam et al., 1986; Gudmundsson, 1993; Gudmundsson and Alerstam, 1998a).

In this study, we placed a tracking radar on the vessel of the Swedish-Russian expedition "Tundra Ecology-94," registering bird migration as the ship moved along the Northeast Passage of the Arctic Ocean, from the Kola Peninsula to the Chukotka Peninsula and back (Grönlund and Melander, 1995; Alerstam and Jönsson, 1999). This paper evaluates the postbreeding migration of tundra birds, which we monitored at 15 different sites between longitude 50˚E and 170˚E during July and August 1994. Results obtained during the same expedition for spring migration during June in the longitudinal sector 45°–105˚E are presented in a separate paper.

This paper (a) summarizes overall tracking radar results (altitudes, speeds, and directions) for all study sites and identified species; (b) presents briefly the migration pattern at each study site; and (c) analyzes the distributions and interrelationships between altitudes, speeds, and directions on the basis of the total data set from all sites combined. We evaluate the observed migration patterns in the light of possible migration routes and orientation principles in the Arctic region and on a global scale and discuss flight strategies in relation to the effects of wind on direction, speed, and flight range.

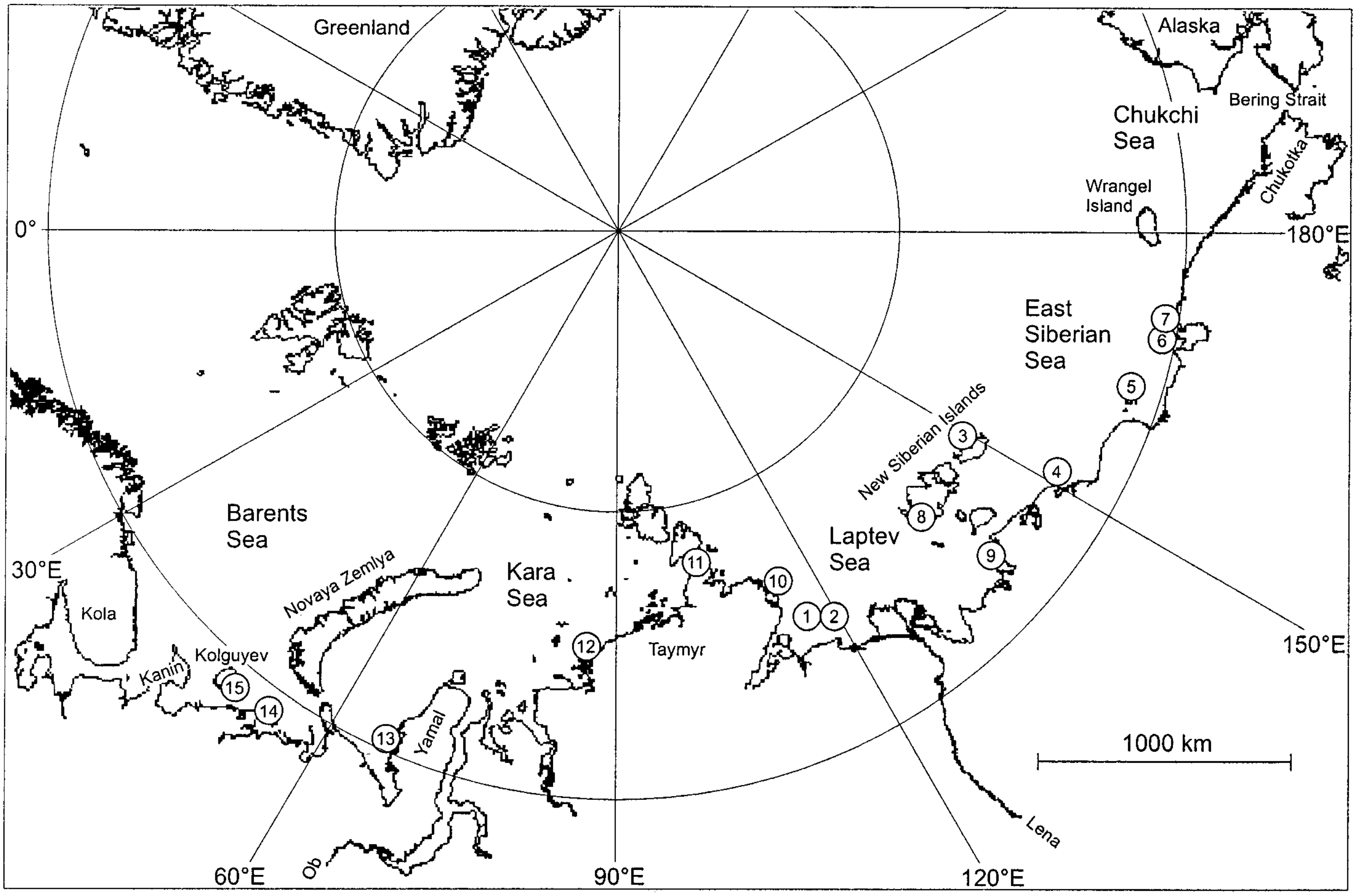

FIG. 1. Radar observations of bird migration were carried out at 15 different sites along the Northeast Passage in July and August 1994. Locations, dates, and general radar information for each site are given in Table 1.

TABLE 1. Radar observation sites along the Northeast Passage in July and August 1994: locations, dates, and general radar tracking information. The sites are plotted in Figure 1.

Site No.	Location	Lat (˚N)	Long (˚E)	Date	No. of tracks	Tracking time (hh:mm)	No. of wind profiles	Radar operation time (hh:mm)
1	SE Taymyr	74.7	115.6	4–5 July	80	4:12	5	12:55
2	Olenyoksi Bay	74.4	119.9	6–8 July	33	1:56	4	09:30
3	N New Siberian Islands	75.7	147.3	11 July	29	2:28	4	11:15
4	Indigirka	72.3	152.3	14–15 July	109	10:22	7	23:50
5	Kolyma	70.8	162.9	18 July	72	5:25	4	12:10
6	Ayon Island	70.3	168.4	20 July	55	4:16	3	09:05
7	Cape Shelagski	70.3	170.5	22–26 July	163	10:12	9	24:50
8	SW New Siberian Islands	74.7	137.8	31 July–2 August	115	8:52	10	27:10
9	Yana	72.4	138.9	3–6 August	106	6:43	6	21:25
10	E Taymyr	76.5	113.5	10–12 August	41	1:49	2	15:54
11	Cape Chelyuskin	77.4	101.9	13–14 August	38	2:13	4	12:26
12	Dikson, SW Taymyr	73.6	80.3	18–19 August	122	4:11	2	16:49
13	W Yamal	70.1	66.5	23 August	36	1:02	0	01:55
14	Pechora	69.0	53.5	24–26 August	66	2:41	5	12:58
15	Kolguyev Island	68.9	50.1	26 August	22	0:50	0	02:40
	Total:				1087	67:16	65	214:54

OBSERVATION SITES AND METHODS

Tracking radar observations with complementary field studies of postbreeding bird migration were carried out at fifteen different sites along the Northeast Passage during the Swedish-Russian Tundra Ecology expedition in 1994. The sites are shown in Figure 1, and locations and dates are given in Table 1. The sites are numbered in chronological order, as the expedition ship moved first eastward from the Laptev Sea, reaching the most easterly site (Site 7) in the East Siberian Sea by the end of July, and then turned westward to follow the Northeast Passage back towards the Atlantic in August. All radar observations were undertaken when the ship was stationary, normally anchored in pack ice or open sea 10–90 km off the nearest tundra shore. Observation sites were chosen in advance, taking into account the needs of the many projects participating in the expedition, including the present project (Grönlund and Melander, 1995).

A tracking radar was placed at the prow of the ice-going expedition vessel *Akademik Fedorov*, with the radar antenna approximately 15 m above sea level (altitudes given in this paper refer to the altitudes above the radar antenna level). This radar operates on a wavelength of 3 cm, with a peak power of 200 kW and pulse duration of 0.5 µs. The nominal beam width is 1.65˚. The minimum range was 600 m, and the maximum useful range was 15–20 km. The maximum tracking error is about ± 50 m in position.

The operator was able to select a target on a range-scope (A-scope) display, and then set the radar to track the selected target automatically. Range, elevation, and bearing to the target were read by computer every two seconds from the radar. The radar was aligned with the long axis of the ship, and readings from the gyrocompass, along with GPS positions, were stored every 60 seconds by computer (radar tracking took place only when the ship was stationary). After taking the ship's direction and exact levelling (see below) into account, we converted the raw data into position and height and calculated track direction, ground speed, and vertical speed of the target.

Winds at low altitude were recorded and stored continuously (every minute) from an anemometer on board the ship. Winds at different altitudes were measured by releasing and tracking helium balloons that carried an aluminum foil reflector. Airspeeds and heading directions of the birds could then be calculated by vector subtraction of horizontal wind velocities at the altitudes at which the birds were flying. A video camera on the radar antenna permitted the operator to locate the wind balloons for radar tracking and calibrate the elevation angle against the horizon in different compass directions.

We systematically scanned for radar echoes of bird flocks from the lowest to the highest elevations to avoid strong bias with respect to altitude or direction in the sample of tracked birds. Hence, we think that the sample of tracks from each site and occasion reflects in a reasonable way the actual distribution of migrating bird flocks with respect to altitude, direction and speed. (When scanning at high elevations, the radar would have permitted detection and tracking of bird flocks travelling as high as 5–8 km above sea level, had any such high-altitude migration occurred.)

On some occasions, one or more field observers on the foredeck of the ship assisted the radar operator. Kept continuously informed via intercom about azimuth and elevation of the radar target, they could visually observe and identify some of the targets using telescopes directed accordingly. Such identifications could normally be made only of targets within a 3–4 km range under conditions of good visibility. About 7% of all targets tracked by the radar were visually observed in this way.

We obtained supplementary field information (nonsystematic notes from ornithologists) from temporary field camps on the tundra at each site. We also obtained such information directly, by making field visits to the tundra camps and by low-altitude helicopter surveys (Alerstam and Jönsson, 1999).

The raw data stored every two seconds from the radar were transformed into rectangular coordinates and averaged over 10 s intervals. For the helium balloon trackings, wind speed and direction were calculated at 30 s intervals, which corresponded to altitude intervals of about 75 m (except the initial height interval from release of the balloon until the first radar reading, which often spanned several hundred metres).

All radar tracks lasting less than 30 s were excluded from the analysis (one 20 s track of identified waders is included). Furthermore, 100 s was the minimum tracking time required for calculation of mean rate of climb/descent (V_z). Because the vertical speed is normally very low, it may be biased by radar tracking errors if the time interval is very short.

Airspeeds and heading directions were calculated for cases where the flight altitude fell within an altitude interval for which we had wind data or did not differ by more than 150 m from the nearest altitude interval with valid wind data. Furthermore, we normally required wind measurement within ± 2 hours from a radar tracking for calculation of airspeed/heading direction. The exceptions were a few cases with stable winds between successive wind measurements over a longer time span, for which we accepted a time difference between bird tracking and wind measurement of up to 3 h 30 min. Of all airspeeds/heading directions, 84% are calculated from wind measurements within 2 h from the time of tracking and 98% within 3 h.

Speeds (ground speed and airspeed) and directions (track and heading direction) were calculated for each 10 s interval of the bird tracks, and subsequently averaged to give the overall mean speed and direction for each track. These overall means are the basis of the present evaluation, and we have not considered the variation in speed/direction within tracks in this paper (normally courses and speeds were straight and steady). Mean and scatter of directions for different samples of tracks have been calculated as mean vector directions and angular deviations, respectively (Batschelet, 1981).

We have omitted results from study sites with ≤ 10 radar tracks from our analysis. Times were recorded in GMT. When necessary, they were later recalculated into exact local time according to the longitude of the relevant site. Times given for migration events at the different sites refer to local times.

RESULTS

A grand total of 1087 radar tracks of migrating birds were recorded at 15 observation sites. The number of tracks varied (range = 22–163) at the different sites (Table 1). Tracks lasted between 30 s (one case of 20 s) and 1280 s, with a mean duration of 223 s and median of 170 s. The total tracking time amounted to 67 h. The total radar operation time (search and tracking) was 215 h, occurring at all hours of local time but with rather less coverage between 0200 and 0700 compared to other times of the day. We focused on recording reliable tracking data (for birds and wind balloons) and did not quantify the number of bird echoes at different sites and times, so our data are not well suited to analyze the time distribution of migration. Still, relating the number of tracks to the radar operation time indicates a somewhat higher level of migration intensity during the evening and night (5.5 tracks per operation hour between 1500 and 0700 local time) than during the late morning and middle of the day (3.9 tracks/h between 0700 and 1500 local time).

Data about altitude, ground speed (V_g), and track direction are available for all 1087 tracks. Valid wind data (cf. above) were available for 903 of the tracks, permitting calculation of airspeed (V_a) and heading direction. Furthermore, speed of climb/descent (V_z) was calculated for the 882 tracks that lasted 100 s or longer. Mean and scatter of altitudes, speeds, and directions are summarized in Table 2 for the different sites and also for main categories (with respect to track direction and in one case to airspeed) at each site.

While the mean altitude was low or modest (300–800 m) at sites 10–13 and 15, it was impressively high (1700–2100 m) at sites 3–7 and 14. Top altitudes at the latter sites reached as high as 3200–4800 m. Mean V_z was close to zero at most sites, except at sites 7 and 8: there it was clearly on the positive side, and many flocks were tracked while gaining height.

Mean airspeed was rather similar (between 12.4 and 15 m/s) at the different sites. However, the birds travelled under widely different wind conditions (the mean wind speed they encountered ranged from 3.2 to 11.4 m/s); this caused a very wide variation in mean ground speed (from 11.7 to 23.1 m/s) at the different sites.

The overall mean track and heading directions were towards E-SE at sites 1–10 and towards SSW-WSW at sites 12–15. However, at most sites the circular distribution of directions showed a rather wide scatter, sometimes with asymmetries and modalities, demonstrating that different categories of migrants were involved (Table 2).

Mean altitudes, speeds, and directions for the radar targets that were identified by species or category are presented in Table 3. The flock sizes given in this table show that, although single birds were sometimes tracked, the vast majority of tracks refer to flocks of migrants.

The two most important groups of migrants in this study are waders (ranging in size from the small phalaropes and *Calidris* species to the larger ruff *Philomachus pugnax*, plovers *Pluvialis* spp., and bar-tailed godwits *Limosa lapponica*) and skuas *Stercorarius* spp. In addition, arctic terns (*Sterna paradisaea*), gulls, ducks, and geese are included among the migrants. For the ducks and geese, the movements recorded in this study presumably reflect mainly moult migration.

Airspeeds of identified targets can help to indicate the composition of migration. However, it should be noted that airspeeds are expected to vary not only between

TABLE 2. Mean and scatter (s.d. = standard deviation, a.d. = angular deviation) of altitudes, speeds (ground speed V_g, airspeed V_a, wind speed V_w, and vertical speed V_z) and directions (track-, heading- and wind directions) of migrating birds tracked by radar at 15 study sites along the Northeast Passage. Summary statistics are given for all tracks at each site, and also for main cohorts with track directions in specified sectors. Data about altitude, ground speed, vertical speed, and track direction are based on the total number of available tracks, while data about wind, airspeed, and heading direction are based on the number of tracks given in parentheses.

Site no.	Category	No. tracks	Altitude (m) Mean (± s.d.)	Altitude (m) Max	V_g (m/s) Mean (± s.d.)	V_a (m/s) Mean (± s.d.)	V_w (m/s) Mean (± s.d.)	V_z (m/s) Mean (± s.d.)	Track dir. Mean (± a.d.)	Head dir. Mean (± a.d.)	Wind dir. Mean (± a.d.)
1	All:[1]	80 (78)	1486 ± 717	3785	21.9 ± 4.2	13.6 ± 2.3	10.4 ± 3.1	0.15 ± 0.47	117 ± 20	131 ± 28	278 ± 21
2	All:[2]	33 (31)	1014 ± 724	2866	17.9 ± 4.1	13.1 ± 1.9	7.8 ± 2.9	-0.02 ± 0.36	113 ± 43	122 ± 45	279 ± 47
	a) NE-sector 50–80°	8 (6)	2070 ± 505	2866	18.9 ± 1.9	13.4 ± 1.6	6.4 ± 0.7	-0.04 ± 0.25	66 ± 11	73 ± 11	243 ± 16
	b) SE-sector 97–159°	22 (22)	0692 ± 386	1989	17.7 ± 3.3	12.8 ± 2.0	8.1 ± 2.5	-0.01 ± 0.39	125 ± 15	128 ± 26	297 ± 44
3	All:[3]	29 (29)	1862 ± 705	3236	12.3 ± 2.1	14.6 ± 2.1	3.2 ± 1.1	-0.11 ± 0.37	93 ± 16	96 ± 13	106 ± 38
4	All:[4]	109 (109)	2116 ± 845	3782	15.8 ± 3.2	13.6 ± 2.1	5.4 ± 2.4	0.04 ± 0.23	113 ± 22	100 ± 18	342 ± 47
	a) E-sector 70–110°	64 (64)	2277 ± 871	3685	16.1 ± 2.6	13.5 ± 2.4	4.4 ± 1.8	-0.01 ± 0.18	99 ± 8	91 ± 11	319 ± 40
	b) SE-sector 111–163°	44 (44)	1897 ± 765	3782	15.5 ± 4.0	13.7 ± 1.5	7.0 ± 2.3	0.09 ± 0.27	133 ± 14	112 ± 12	15 ± 40
5	All:	72 (62)	2119 ± 1074	4447	16.8 ± 4.3	13.1 ± 2.4	5.0 ± 2.8	0.11 ± 0.22	92 ± 39	101 ± 42	231 ± 52
	a) E-sector 68–138°	64 (54)	2302 ± 990	4447	16.8 ± 4.4	12.6 ± 1.9	5.2 ± 2.8	0.11 ± 0.21	93 ± 14	102 ± 18	236 ± 40
	b) W-sector 215–329°	8 (8)	655 ± 358	1167	17.2 ± 3.1	16.3 ± 2.8	4.2 ± 2.7	0.12 ± 0.29	279 ± 32	285 ± 42	90 ± 44
6	All:[5]	55 (45)	1861 ± 830	3552	19.0 ± 3.1	12.4 ± 1.8	6.8 ± 2.5	0.15 ± 0.19	109 ± 9	108 ± 14	291 ± 19
7	All:	163 (142)	1815 ± 1222	4816	23.1 ± 5.4	13.7 ± 3.8	10.7 ± 4.1	0.27 ± 0.40	101 ± 34	97 ± 42	282 ± 35
	a) Va > 20m/s	13 (13)	669 ± 348	1609	29.9 ± 4.9	22.2 ± 1.7	9.6 ± 3.8	0.24 ± 0.33	67 ± 18	63 ± 18	263 ± 40
	b) E-sector 32–162°	142 (121)	1952 ± 1221	4816	22.8 ± 4.9	12.5 ± 2.4	11.1 ± 4.1	0.27 ± 0.41	104 ± 23	102 ± 33	282 ± 30
	c) W-sector 233–330°	8 (8)	1240 ± 1049	3091	17.6 ± 3.9	17.7 ± 2.7	7.4 ± 3.3	0.31 ± 0.28	276 ± 35	288 ± 19	313 ± 64
8	All:	115 (113)	942 ± 552	2583	18.7 ± 6.4	14.3 ± 3.4	11.4 ± 5.2	0.24 ± 0.48	117 ± 61	153 ± 62	265 ± 29
	a) E-sector 42–118°	49 (47)	838 ± 399	2029	23.3 ± 5.1	11.7 ± 2.1	14.3 ± 6.0	0.35 ± 0.38	84 ± 21	104 ± 22	250 ± 31
	b) SE-sector 121–183°	38 (38)	795 ± 539	2463	18.4 ± 2.7	14.8 ± 2.3	8.3 ± 2.7	0.22 ± 0.47	150 ± 20	171 ± 30	284 ± 17
	c) W-sector 197–010°	28 (28)	1321 ± 637	2583	11.2 ± 4.3	18.0 ± 2.8	10.9 ± 3.7	0.07 ± 0.59	280 ± 45	271 ± 23	261 ± 24
9	All:	106 (105)	1003 ± 825	3165	18.8 ± 5.9	15.0 ± 2.4	9.2 ± 4.8	-0.01 ± 0.45	83 ± 56	119 ± 60	230 ± 32
	a) E-sector 48–136°	78 (78)	1127 ± 868	3165	19.7 ± 5.0	15.0 ± 2.2	8.8 ± 4.7	0.01 ± 0.44	95 ± 22	114 ± 28	234 ± 27
	b) W-sector 205–315°	20 (19)	591 ± 561	2546	14.5 ± 7.1	15.5 ± 2.8	9.0 ± 4.5	-0.01 ± 0.43	287 ± 26	265 ± 18	221 ± 39
	c) N-sector 323–035°	8 (8)	831 ± 610	1928	20.8 ± 6.0	13.6 ± 3.5	13.7 ± 4.4	-0.31 ± 0.52	358 ± 23	332 ± 27	201 ± 37
10	All:[6]	41 (22)	613 ± 284	1818	19.5 ± 4.2	13.6 ± 3.4	5.7 ± 2.7	-0.12 ± 0.33	94 ± 16	86 ± 29	283 ± 25
11	All:	38 (28)	712 ± 554	2186	15.9 ± 3.5	14.3 ± 3.5	5.1 ± 2.0	-0.04 ± 0.66	357 ± 65	345 ± 58	23 ± 56
	a) NE-sector 6–82°	21 (14)	510 ± 395	1910	15.5 ± 3.3	14.4 ± 3.0	5.3 ± 2.2	-0.15 ± 0.53	44 ± 20	36 ± 17	331 ± 61
	b) W-sector 228–358°	17 (14)	960 ± 628	2186	16.4 ± 3.7	14.3± 4.0	4.9 ± 1.9	0.10 ± 0.79	268 ± 32	281 ± 33	046 ± 29
12	All:[7]	122 (78)	303 ± 306	1728	13.9 ± 3.2	13.8 ± 3.3	3.4 ± 1.4	0.00 ± 0.36	253 ± 41	240 ± 46	151 ± 44
	a) S-sector 149–202°	13 (7)	194 ± 125	421	11.1 ± 2.8	12.6 ± 2.4	1.9 ± 1.2	-0.07 ± 0.39	174 ± 15	162 ± 12	191 ± 33
	b) W-sector 218–308°	96 (59)	314 ± 296	1653	14.6 ± 2.8	14.4 ± 3.0	3.7 ± 1.3	-0.01 ± 0.33	254 ± 17	242 ± 23	147 ± 41
	c) N-sector 316 –032°	12 (6)	342 ± 487	1728	11.6 ± 3.6	10.2 ± 3.5	2.8 ± 1.3	0.10 ± 0.55	352 ± 27	360 ± 40	153 ± 57
13	All:	36 (0)	753 ± 529	2630	20.3 ± 3.4	-	-	0.00 ± 0.41	203 ± 20	-	-
14	All:[8]	66 (57)	1717 ± 1304	4755	20.7 ± 5.4	13.9 ± 3.3	8.5 ± 2.7	-0.09 ± 0.54	255 ± 45	258 ± 43	89 ± 11
	a) S-sector 149–217°	13 (9)	903 ± 820	2566	18.2 ± 6.5	14.8 ± 4.9	7.0 ± 2.8	-0.08 ± 0.43	170 ± 36	126 ± 33	79 ± 11
	b) W-sector 225–344°	50 (43)	2006 ± 1313	4755	21.7 ± 4.7	13.7 ± 3.1	8.7 ± 2.6	-0.04 ± 0.27	265 ± 17	261 ± 26	90 ± 11
15	All:[9]	22 (4)	681 ± 461	2065	11.7 ± 2.3	-	-	0.04 ± 0.19	211 ± 68	-	-
	a) SE-sector 120–195°	8 (-)	699 ± 670	2065	11.9 ± 2.6	-	-	-0.09 ± 0.25	151 ± 22	-	-
	b) W-sector 234–328°	11 (-)	688 ± 346	975	11.0 ± 2.1	-	-	0.11 ± 0.10	267 ± 35	-	-

[1] Including 79 tracks in sector 82–169° and one track at 210°.

[2] Including tracks in sectors a) and b) and 3 tracks in sector 238–285°.

[3] Including 28 tracks in sectors 58–112° and one track 142°.

[4] Including tracks in sectors a) and b) and one track 291°.

[5] Including 55 tracks in sector 92–134°.

[6] Including 41 tracks in sector 40–140°.

[7] Including tracks in sectors a), b) and c) and one track at 92°.

[8] Including tracks in sectors a) and b) and 3 tracks in sector 12–52°.

[9] Including tracks in sectors a) and b) and 3 tracks in sector 8–78°.

species, but also between individuals and flocks of a given species, depending on wind, altitude, climb/descent rate, and flock size (Pennycuick, 1975, 1989; Hedenström and Alerstam, 1995). This means that airspeed is diagnostic of species or groups only at a very crude level.

The slowest airspeeds of identified targets (9–14 m/s) referred to arctic tern and grey phalarope *Phalaropus fulicarius* (Table 3). The total range of airspeeds for unidentified waders was 10–18 m/s. Large-sized species were probably responsible for the speeds at the upper end of this spectrum, as indicated by the measurements of identified ruffs and bar-tailed godwits, which showed airspeeds of 15–18 m/s. Among the waders, those spotted at very high altitudes (>3 km) in flock formations had the highest airspeeds, about 18 m/s. The most probable species in these flocks were grey plover *Pluvialis squatarola* and/or bar-tailed godwit. However, no definite identification was possible since the birds, spotted vertically above the observer at immense height, were shining pure white against the clear blue sky because of the strong illumination reflected from the pack ice below.

Airspeeds of skuas were between 12 and 18 m/s, with an overall mean close to 15 m/s (Table 3). Radar echoes from skuas could in some cases be provisionally distinguished from echoes from waders because of the relatively slow wingbeats of the skuas. Such radar echo signatures indicated that skuas made up a significant fraction of the migrants at many sites, but there is little doubt that waders comprised the absolute majority of migratory birds at all sites in this study. It is important to note that skuas migrate also at very high altitudes: a formation of 26 pomarine skuas was identified at an altitude of 1932 m, and a flock of 4 unidentified skuas at 3019 m!

Fastest among the identified species were the long-tailed duck *Clangula hyemalis* and Steller's eider *Polysticta stelleri*, both with airspeeds of 22 m/s (Table 3). Moult migration of mainly Steller's eider drakes comprised a small but significant part of the migration recorded at the easternmost site (Site 7; cf. below).

Migration Patterns at the Different Sites

In this section we give an account of the observations at each site, referring to Table 2 for the summary statistics of altitudes, speeds, and directions for the different sites and cohorts.

Site 1: Ship position was in pack ice far offshore in Khatanga Bay, 100 km from the Taymyr east coast to the west and 110 km from the mainland coast to the south. The weather was sunny, with little cloudiness and very good visibility.

At this site we encountered an early wave of postbreeding migration on 4 and 5 July. Flocks were travelling towards E-SE at varying heights, mostly 500–2500 m, in strong westerly tailwinds. Most of the flocks (76%) were climbing slowly. Because of the tailwinds, which increased with altitude, ground speeds were high, reaching 26–32 m/s for the fastest fraction (19%) of migrants. According to visual

TABLE 3. Radar tracking data for migrating birds identified to species or category. Data about altitude, ground speed, vertical speed, and track direction are based on the total number of available tracks, while data about airspeed and heading direction are based on the number of tracks given in parentheses. Time refers to the total tracking time. Mean and range (in parentheses) are given for the different altitude, speed, direction, and flock size variables.

Species/group	No. of tracks	Time (s)	Altitude (m)		Vertical speed (m/s)		Ground speed (m/s)		Airspeed (m/s)		Track direction (degrees)		Heading direction (degrees)		Flock size	
Brent goose	1	930	506		0.31		22.8		16.3		140		152		14	
Steller's eider	1	310	369		-0.07		32.7		22.3		47		48		30	
Long-tailed duck	1	180	428		0.59		30.7		22.2		56		58		3	
Ruff	4	2310	479	(141–1030)	0.18	(0.04–0.38)	12.8	(10.6–14.2)	16.6	(15.0–18.6)	298	(286–315)[1]	273	(269–280)[1]	9.5	(2–17)
Bar-tailed godwit	1	50	61				16.4		15.9		242		225		20	
Grey phalarope	8	1980	530	(34–1231)	0.02	(-0.23–0.29)	19.4	(16.1–25.1)	12.7	(9.1–14.7)	105	(75–116)	113	(89–131)	3.1	(1–7)
Red-necked phalarope	1	230	283		0.24		15.1		13.3		242		226		3	
Waders, eastbound	15	5630	1163	(385–2740)	0.19	(-0.19–1.30)	19.0	(14.6–26.5)	13.3	(10.0–17.4)	108	(95–122)	113	(75–147)	8.3	(2–18)
Waders, high-alt (>3km)	3	2500	3534	(3477–3592)	-0.02	(-0.07–0.01)	20.3	(20.0–20.7)	17.7	(17.0–18.4)	101	(95–109)	86	(82–89)	53.3	(30–70)
Waders westbound	10 (8)	1340	236	(51–397)	-0.08	(-0.69–0.21)	16.7	(13.2–20.6)	14.9	(12.0–17.4)	254	(237–282)	244	(218–276)	42.1	(4–100)
Waders, S-W-N-bound	4	1320	356	(0–787)	-0.14	(-0.43–0.03)	14.7	(10.0–16.6)	14.9	(12.5–18.5)					9.3	(2–18)
Pomarine skua	13 (11)	5010	452	(2–1932)	0.22	(-0.18–0.85)	18.3	(10.7–24.7)	14.9	(11.5–17.5)	138	(87–178)[2]	152	(130–196)[2]	6.8	(1–26)
Long-tailed skua	2	1360	908	(734–1081)	0.83	(0.37–1.28)	18.4	(16.0–20.8)	14.5	(12.4–16.6)	135	(126–143)	159	(152–165)	1.5	(1–2)
Unidentified skua	6 (3)	1080	780	(127–3019)	0.35	(-0.34–1.07)	18.0	(10.7–23.0)	15.8	(13.8–17.9)	165	(114–193)[3]	178	(169–187)[3]	2.5	(1–6)
Herring gull	2 (1)	200	208	(101–315)	0.24		13.6	(11.1–16.0)	13.2		30	(12–47)	28		5.5	(1–10)
Kittiwake	3 (2)	1060	293.7	(92–542)	-0.17	(-0.35–0.12)	15.9	(10.3–23.0)	13.6	(13.5–13.7)					5.3	(2–11)
Arctic tern	1	500	522		0.36		13.8		11.2		101		130		9	

[1] One track excluded, with track direction 64° and heading direction 108°.

[2] One track excluded, with track direction 290° and heading direction 285°.

[3] One track excluded, with track direction 10° and heading direction 310°.

field observations, the migrants were mainly waders in small flocks of 2–7 individuals (10 identified echoes). A prominent species was the grey phalarope (two identified echoes, and additional flocks of this species, not tracked by radar, were recorded by observers on the ship), and other highly probable wader species involved in the migration stream were curlew sandpiper *Calidris ferruginea* and sanderling *Calidris alba*. Although waders were strongly dominant, skuas also took part in the migration (one echo was identified as a pair of pomarine skuas).

Site 2: Ship position was in pack ice 100 km north of the mainland tundra coast at Olenyoksi Bay. A regular but rather sparse migration took place on all three observation days. On 6 July, with sunshine and clear skies but strong SE winds at low altitudes (an approaching depression), sparse migration occurred in the NE-E sector at rather high altitudes (1100–2900 m), where almost due tailwinds prevailed. On 7 and 8 July, after the depression had passed, migration was a bit more intensive, mainly directed towards the SE quadrant at relatively low altitudes (mostly <1000 m), where SW-NW winds were blowing (winds at higher altitudes were easterly). On 8 July, migration took place above widespread, low-level fog over the pack ice. A few flocks were travelling in westerly directions at this site.

No radar echoes were identified, but observations at field camps on the tundra provided valuable information: Many waders, such as pectoral sandpiper *Calidris melanotos*, grey phalarope, curlew sandpiper, dunlin *Calidris alpina*, and sharp-tailed sandpiper *Calidris acuminata*, were assembling in small postbreeding migratory flocks at tundra pools. Some of these flocks were even seen to depart (E-ENE departures of pectoral sandpiper flocks and easterly departures of grey phalaropes were observed). All these species are likely to be included in the eastbound migration recorded by radar. Possibly there is a prevalence for ENE-E courses among pectoral sandpipers (and partly also among grey phalaropes) and for ESE-SE courses among the other species. There were also field reports about small migratory flocks of ruff and little stint *Calidris minuta*, which seemed to be inclined to move towards W and SW, respectively.

Site 3: Ship position was at the edge of a polynya about 30 km north of Novaya Sibir Island, the easternmost of the New Siberian Islands. A high-pressure situation prevailed on 11 July, with clear skies, sunshine, excellent visibility, and weak winds. Migration increased gradually during the afternoon and early night. Mean direction was almost due east, with 12 tracks directed slightly to the north of east and 17 tracks slightly to the south of east. Altitudes were highly scattered, mostly 1000–3000 m, with weak opposing winds at all levels.

According to field observations of postbreeding migratory flocks on the tundra of the New Siberian Islands (from field camps on Faddeyevski Island), the primary candidate species to make up the migration are pectoral sandpiper (field records include one flock migrating ENE), turnstone *Arenaria interpres*, grey phalarope, sanderling, curlew sandpiper, and knot *Calidris canutus*. Bar-tailed godwits, grey plovers, and Pacific golden plovers *Pluvialis fulva* were also recorded. There were also flocks of brent geese *Branta bernicla nigricans* on the islands, but these did not show any migratory tendencies.

The migration pattern recorded at this site is of particular interest because it indicates a direct migration route across 1800–3000 km of the Arctic Ocean towards Alaska and/or High Arctic Canada, running at least 500 km north of the tundra coast of East Siberia.

Site 4: Ship position was in pack ice about 100 km ENE of the Lopatka Peninsula and about 130 km NNE of the Indigirka River delta. On 14 July, low-level fog prevailed until late in the night, when the sky became totally clear with excellent visibility and sunshine. This weather lasted throughout 15 July. Winds were rather weak at high altitudes, mainly from NNE on 14 July and from W-NW on 15 July, while it was calm at the lowest altitudes.

During the evening of 14 July, migration, mainly towards E-ESE, was massive from 2100 and onwards during the night. Radar echoes of migrating bird flocks were recorded at a remarkably high density. It was provisionally guesstimated that as many as 100 000 migrants may have passed the ship within a frontal width of 10–15 km during this wave of mass migration.

Migration occurred mainly at very high altitudes, mostly 1500–3000 m, with a regular passage as high as 3000–3800 m. The migrants were assisted by the winds, which increased their airspeed by 2–3 m/s.

Five targets were identified as flocks of waders, with 14–70 individuals flying in formation, all at high altitudes. The three highest flocks, at altitudes >3000 m, were probably large-sized waders like grey plover or bar-tailed godwit. Field observers recorded large numbers of resting waders on the tundra and at the coast of the Lopatka Peninsula. This peninsula was probably a concentration area for birds preparing for easterly departures. The following species were recorded in the hundreds or thousands and also in migratory flocks showing tendencies toward eastward movements: grey phalarope, bar-tailed godwit, grey plover, pectoral sandpiper, and long-billed dowitcher *Limnodromus scolopaceus*. Small flocks of pomarine skua were also seen migrating eastward.

Site 5: Ship position was in dense pack ice about 120 km ENE of Krestovski Head and 140 km NNE of the Kolyma River outlet. The tracks recorded at this site are plotted in Fig. 2.

Low-level fog prevented visual observations from the ship. Intensive migration took place above the fog, where clear skies and sunshine prevailed, until late at night; then a front with rain approached from the west, and migration came to a halt. Altitudes were high, mostly 1500–4000 m, where moderate SW-W winds prevailed. During the two hours prior to the start of raining, migration intensity was rapidly reduced: the flocks were migrating below a cloud ceiling that was progressively lowered from 2000 m to 500 m as the front approached. Mean direction at this site

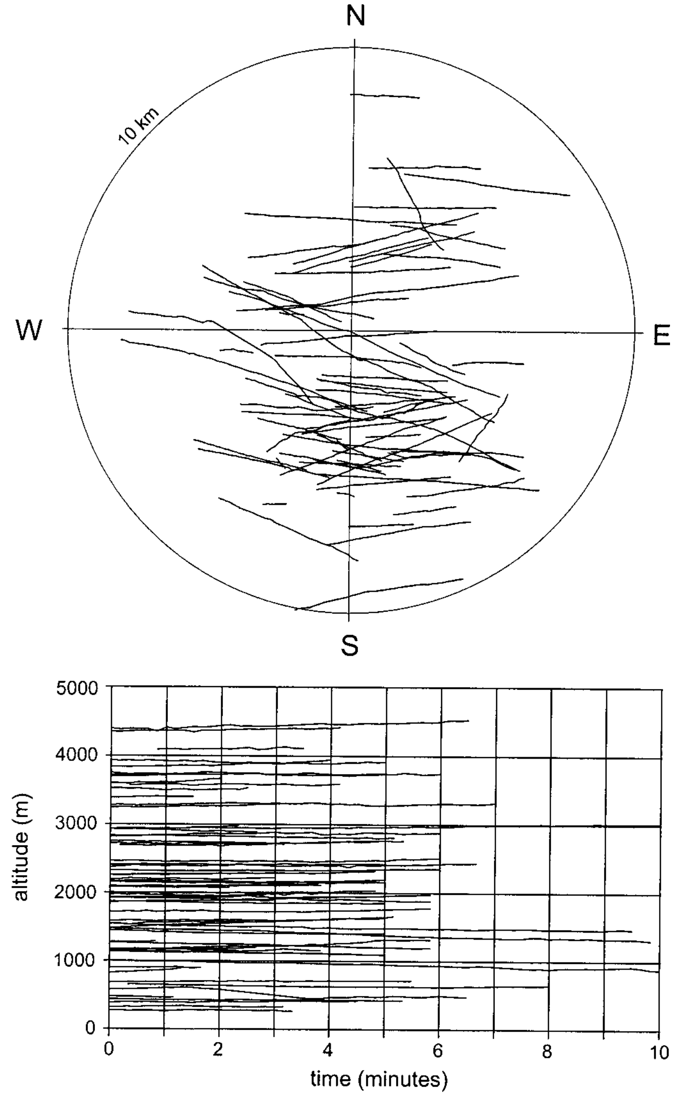

FIG. 2. Plots of radar tracks (n = 72) of migrating flocks of birds at Site 5 (Kolyma) on 18 July 1994. The upper figure shows the geographic pattern of migration, plotted in relation to the position of the ship at the centre. The lower figure shows altitudes in relation to tracking time. The vast majority of birds (n = 64) migrated in an easterly direction, but a few flocks (n = 8) were travelling on westerly courses (cf. Table 2).

was almost due east, with 28 flocks travelling slightly north of east and 36 flocks slightly south of east. At lower altitudes, below 1200 m, there were easterly winds and sparse migration in westerly directions.

The prominent high-altitude easterly migration was of the same type recorded at the preceding site (and the two following sites), with almost identical distributions of airspeeds. This type of migration was probably dominated strongly by waders, with pomarine skuas also taking part in the movements to a significant degree.

Site 6: Ship position was in dense pack ice about 30 km north of Ayon Island. Above low-level fog or thin clouds, there were clear skies, sunshine, and moderate WNW winds. The radar observations revealed a continued (cf. preceding sites) very intensive easterly flow of migrants, on this occasion within the sector 90–130°, with a fairly uniform height distribution between 1000 and 3000 m. Many flocks were climbing slowly, 0–0.4 m/s, in almost due following winds, which gave an average tailwind assistance of about 7 m/s.

Four targets were identified as wader flocks (flock size 8–14 individuals). A number of flocks of grey phalaropes migrating eastwards were observed from the ship, and flocking of grey plovers was reported from the tundra.

Site 7: Ship position was in dense pack ice 15 km north of Cape Shelagski, with Long Strait and Wrangel Island about 320 km to the E and ENE, respectively. Bird migration, monitored during five days (22–26 July) at this site, built up to a peak on 24 and 25 July: a mass migration similar in magnitude to that at Site 4 on 14–15 July.

The period 23–26 July was characterized by clear skies and sunshine. On 25 and 26 July, the warm sector associated with a depression to the north moved over the study site, generating warm southerly winds that caused a low-altitude inversion with haziness. The birds travelled above this inversion in the flow of west winds. The massive migration wave had come to an almost complete end on 26 July, even though weather was still favourable and sunny (but with greatly reduced wind forces).

Tailwinds were extremely strong (15–20 m/s) during the night of 23–24 July (a depression was passing north of the site), when moderate easterly migration took place with very high ground speeds of 25–30 m/s (even a few cases with ground speeds exceeding 30 m/s were recorded). Favourable westerly tailwinds continued on the two following days of intensive migration, although wind forces were reduced to about 10 m/s. Migration heights were highly variable, with many flocks flying very high (3000–4000 m), up to the maximum height recorded in this study (4816 m).

Three main categories of migrants could be distinguished:

1. Flocks travelling with high airspeeds (>20 m/s) and with courses in the sector 40–90° at altitudes mainly between 200 and 1000 m made up the first category. This was probably moult migration, mainly of Steller's eider drakes, and long-tailed ducks may also have been involved (one radar track of each species was identified, cf. Table 3). E-NE migration of Steller's eiders was observed from the ship, mostly at low altitudes, and many thousands of Steller's eider drakes were observed along the Chukotka coast during a helicopter survey.

2. The dominating pattern was the intensive migration towards the sector E-ESE, with some flocks flying towards ENE and SE. About half of the flocks travelled on courses >100°, and these courses indicate flight routes across land towards the Bering Strait. Grey phalaropes, grey plovers, and knots were seen migrating eastwards past the ship. Two radar echoes were identified as high-altitude flocks of pomarine skua (at 1932 m) and unidentified skua (at 3019 m), respectively.

3. Sparse movements in westerly directions may have been ruff, ducks (there were two cases with airspeeds >20 m/s), or waders in return flight.

Site 8: Ship position was in loose pack ice 15 km from the southwestern shore of Kotelny Island (New Siberian Islands). In spite of consistently westerly winds, there was a wide scatter of directions, with migration taking place in both following and opposing winds. On 31 July, a day with sunshine and some high and thin clouds, bird migration took place mainly towards ENE in remarkably strong SW winds, about 20 m/s (an intensive depression was passing north of the observation site). Ground speeds of migrants approached 30 m/s at altitudes mostly below 1000 m. Migration stopped when a weather front with rain arrived from the west at midnight. On 1 August, migration took place above low-level fog and clouds in easterly, southerly, and westerly directions, until weather again deteriorated and rain started. On 2 August skies were clear, with some snow showers, sunshine, and moderate westerly winds. Migration was intensive, mostly towards ESE-SE at rather low altitudes (<1000 m), and many radar echoes were identified as flocks of pomarine skua.

Migration could be provisionally divided into three main categories:

1. Easterly migration occurred in the sector 40–120°, with the migrants climbing in strong (on 31 July very strong) tailwinds and crossing the New Siberian Islands. Two of these radar echoes were identified, one small flock of grey phalaropes and one flock of arctic terns. The slow airspeeds indicate that mainly small waders (and terns) were involved in this category. The most probable candidate species, according to observations of migratory flocks at the field camps on Kotelny Island, were grey phalarope, turnstone, sanderling, curlew sandpiper, and grey plover.

2. Migration in the sector SE-S consisted mainly of pomarine skuas (8 flocks identified), but also of long-tailed skuas *Stercorarius longicaudus* (2 flocks identified) and brent geese (1 flock identified). In addition, one flock of waders, probably knot, with a course due south was among the identified radar tracks in this category. The flight paths of the skuas were probably guided in many cases by the coast of Kotelny Island (running NW-SE); the birds were flying some distance off and parallel with the coastline of this island, presumably veering to more ESE courses as they reached the southern tip of the island.

3. Migration in the W sector was quite significant, especially on 2 August above fog and low clouds, when the migrants made slow progress into rather strong opposing winds. According to the field observations at Kotelny Island, flocks of knot showed clear tendencies of migrating towards the sector S-W. Some skuas were also suspected to migrate in westerly directions.

Site 9: Ship position was in open water 20 km west of Churkin Point in the Yanski Bay. Weather was characterized by clear skies, sunshine, high visibility and S-WSW winds on all observation days.

Three groups of migrants were distinguished:

1. Easterly migration took place in the sector NE-SE, mostly below 1000 m, but on one day (6 August) some flocks travelled above 2000 m, up to about 3000 m. If these birds maintained their courses, they must have flown across the coastal tundra towards the Indigirka and Kolyma River deltas. Large numbers of resting wader flocks were reported from the field camps on the coastal tundra, with juveniles comprising a large proportion of the migrants for the first time in the season. According to the field reports, the most important species to take part in the easterly movements were grey phalarope, curlew sandpiper, pectoral sandpiper, dunlin, sharp-tailed sandpiper, grey plover, and also ruff and little stint (see below). Seven radar echoes were also identified as flocks (1–15 individuals) of small or medium-sized waders.

2. A significant fraction of the migrants travelled on westerly courses in the sector SSW-NW, mostly below 1000 m in cross- or headwinds. Two species that were numerous on the tundra showed tendencies to migrate in westerly directions, little stint (mainly towards SW) and ruff (towards W-NW). Four radar echoes were identified as waders in this category: one flock (10 individuals) of small waders (possibly little stints) moving towards 205°; one pair of ruff moving towards 286°; and two flocks (4 and 17 individuals) of unidentified waders in the same size class as ruffs, with courses towards 296° and 315°. However, field camps also reported important easterly migration tendencies by both juvenile ruff and little stint.

3. A few flocks were moving in northerly directions, and one of the echoes was identified as a flock of 7 medium-sized waders. These movements may have been affected by the coastline to the east, the birds flying north to remain over the sea. Skuas were recorded in negligible numbers in the area.

Site 10: Ship position was at the pack ice edge east of Taymyr Peninsula, 13 km off the nearest island and about 30 km off the mainland coast. Weather was mostly cloudy and sometimes foggy, with temperature fluctuating around 0°C. Northwesterly winds (5–12 m/s) prevailed on 10–11 August, turning to southerly winds on 12 August.

Migration intensity was low, with all tracks showing easterly directions in fair tailwinds. The birds were on the move above fog and low clouds (average altitude of tracks was 613 m), rendering identification of targets impossible. Visual observations of bird movements from the ship indicated that mainly pomarine skuas, king eiders, and arctic terns were migrating towards the east.

Site 11: Ship position was in pack ice 8 km to the west of the northernmost Taymyr coast. This coast runs from SW to NE, with Cape Chelyuskin situated 65 km to the northeast of the ship. Weather was foggy, with low clouds and some snowfall. Winds were weak and variable on 13 August, but increased in strength and turned to a westerly direction on 14 August.

Migration was in two sectors: NE (6–82°) and W (231°–358°). Migration in the NE sector was predominant after the winds turned to west on 14 August. The average altitude of tracks was 510 m in the NE sector and 960 m in the W sector.

The species composition was quite mixed. Two tracks were identified as a flock of 3 kittiwakes *Rissa tridactyla* and a flock of 10 herring gulls *Larus argentatus*, respectively, both on NE tracks. From the ship, several flocks were observed on migration: a flock of 4 pomarine skuas (towards NNE) and another with 2 individuals (N), one long-tailed skua (N), a flock of 5 Sabine's gulls *Larus sabini* (NE) and another with 3 individuals (ENE), and a flock of 8 turnstones heading SW.

Site 12: The ship was anchored in open water 8 km NW off Dikson, SW Taymyr, from the afternoon of 18 August until noon on 19 August. Weather was fine, with weak southeasterly winds (3–5 m/s), overcast sky (cloud base 400–600 m), and good visibility.

After a rather low migration intensity in the afternoon of 18 August (dominated by skuas; five out of six identified tracks), a mass migration of waders began in the early morning, peaking between 0700 and 1000 and continuing until noon. The waders migrated WSW along the coast, over both land and sea, at low altitudes (mostly 0–500 m). Average altitude for 122 radar tracks was 303 m, with a maximum altitude of 1728 m. Ground speeds and track directions were very well defined, with means ± standard deviations at 13.9 ± 3.2 m/s and 253 ± 41˚, respectively.

Because of the low altitude of migration and good visibility, the birds could be easily observed from the ship. A total of 456 flocks (9590 individuals) were registered, and 1270 individuals were identified to species. Little stint was the most numerous species among the identified birds (54% of total), followed by dunlin (10%), sanderling (9%), knot (7%), and bar-tailed godwit (7%). The remaining 13% were curlew sandpipers, red-necked and grey phalaropes, ruffs, grey plovers, and turnstones.

Site 13: Ship position was in open water about 25 km off the west coast of the Yamal Peninsula. Weather was favourable for migration, with clear skies, sunshine, and winds from NNE.

The radar was operated during only two hours on 23 August, when a massive S-SW migration (mainly SSW along the coast) took place at variable altitudes, mostly 400–700 m (max 2630 m). The birds attained fast ground speeds in favourable tailwinds (9–10 m/s at sea level; no wind profile available).

No tracks were identified, and only two flocks of waders (3 *Pluvialis* sp. heading W and 15 *Numenius* sp. heading SW) were observed from ship. Intensive visual observations immediately after the ship began moving westwards from the coast gave no results, indicating that the migration was probably concentrated in a rather narrow corridor along the coast. Migratory movements observed at a tundra field camp on the nearby Yamal coast on 22 and 23 August comprised brent geese arriving from the north making a stopover on coastal wetlands and a continuous flow of wader flocks moving northward along the coast. The waders, mainly ruffs but also little stints and a few red-necked phalaropes, were flying low and into the winds on both days.

Site 14: The ship was anchored in open water 8 km from the shore (Pechora) on 24 to 26 August. Weather was cloudy (cloud base 400–800 m), temperature was 5–6˚C, and easterly winds (5–9 m/s) prevailed throughout the stay.

Migration was mainly in the W sector (n = 50, 225–334˚) and S sector (n = 13, 149–202˚) with scattered flocks in other directions. Altitude of tracks in the W sector was high (mean 2000 m, maximum 4755 m), but lower in the S sector (mean altitude 900 m).

The only identified track referred to a low-flying herring gull. From the ship, one long-tailed skua and one black-throated diver *Gavia arctica* were observed heading west, and a flock of ducks was seen migrating towards the east. In addition, arctic terns were heard in or above clouds.

Site 15: Ship position was 5 km southeast of Kolguyev Island. Radar was operated during the late night of 26 August. Winds were weak (3–5 m/s) from the west and cloud base was 600 m.

Migration intensity was high, but echoes were weak, indicating that targets were single birds or small flocks. Some targets showed echo patterns suggesting single passerines. Movements were in the SE sector and the W sector, mainly at altitudes of 700–900 m, in or above clouds. Because of darkness, no identification of targets was possible.

Distributions of Track, Heading, and Wind Directions

Total distributions of track, heading, and wind directions are shown in Figure 3. All three distributions are bimodal, with peaks in easterly and westerly sectors. Summing up the number of tracks in an E sector (30–150˚), W sector (210–330˚), and in the intervening N/S intervals (330–30˚ and 150–210˚), one finds that 67% of track directions fall in the E sector, and 23% in the W sector, while only 11% belong to the N/S group (with 8% and 3% in the southerly and northerly subsectors, respectively). The distribution of heading directions between these sectors is virtually identical with that of track directions.

In contrast, wind directions show a reversed distribution (note, however, that wind direction is defined in a reverse way, as the direction from which the wind is blowing) with W winds dominating (67%), E winds occurring in 19% of the cases, and N/S winds in 14% (with 6% in the southerly subsector and 8% in the northerly subsector). To a large degree, the distribution of wind directions in our data set reflects the propensity of the birds for migrating in following winds. E migration (which dominated at easterly sites, where the most radar tracks were recorded; cf. Table 1) took place mainly in westerly winds, and vice versa for W migration.

Migratory directions differed between study sites as summarized in Figure 4, where the sites have been arranged according to longitude. This figure shows that there is a major migratory divide in the longitudinal zone around Site 11, with W migration dominating at the westerly sites 12–15 (long. 50–80˚E) and E migration at the

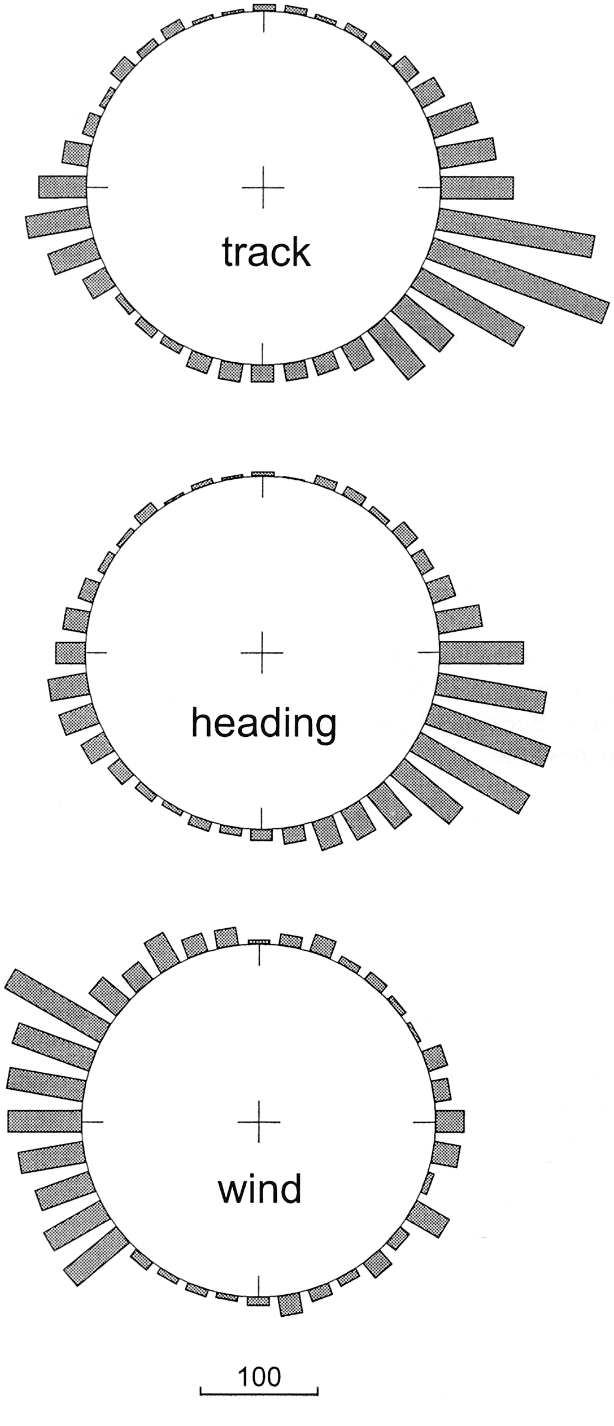

FIG. 3. Distribution of track directions (n = 1087), heading directions (n = 903), and wind directions (n = 903) for the total sample of radar tracks of migrating birds at the Northeast Passage. Scale bar indicates n = 100 tracks.

easterly sites 1–10 (long. 114–171˚E). Of the total sample of track directions at sites 12–15, 70% fell in the W sector, 6% in the E sector, and 24% in the N/S sector. For sites 1–10, the corresponding total distribution of track directions was 7% (W), 87% (E), and 6% (N/S).

The distribution of track directions within the modal E and W sectors at the different sites is presented in Table 4. The most important features of E migration (Table 4a) are the following:

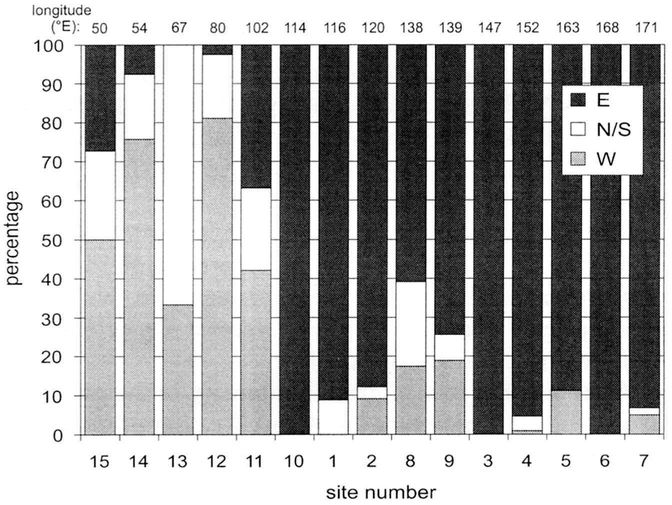

FIG. 4. Proportion of track directions of migrating birds in an E-sector (30–150˚), a W-sector (210–330˚), and the intervening N/S-sectors (300–30˚ and 150–210˚) at the 15 study sites. Sites are arranged according to their longitudinal position from west to east.

The main stream of E migration at sites 1–10 was directed in the ESE sector (90–120˚), forming a migratory highway running broadly in parallel with the East Siberian tundra coast.

ENE migration (60–90˚) was significant at most of these sites (1–10), comprising 21% of the total E migration. These track directions in the ENE sector provide strong indications of long-distance flights between Siberia and North America across vast expanses of Arctic Ocean pack ice.

Low proportions of ENE migration at sites 1, 4, and 6 and high proportions of SE migration at sites 2, 4, and 8 may be related to wind effects and topography (cf. above about leading line effect at Site 8).

The sparse easterly migration at sites 11–15 was directed mainly towards NE and ENE. This to a large degree reflected the situation at Site 11, where the eastbound migration was shifted to northerly courses because of topographical influence (cf. above).

Concerning W migration (Table 4b), the orientation was closely similar between sites 11, 12, 14, and 15, with most tracks in the WSW sector (240–270˚). At Site 13 (W Yamal), the pattern was different, with movements concentrated towards SSW (out of 36 tracks from this site, 24 fell in the sector 170–210˚ and only 12 in the range 210–246˚ included in Table 4b). W migration at locations east of Taymyr (sites 1–10) differed clearly from the corresponding migration west of Taymyr, in that directions towards WNW or even NW were much more common east of Taymyr (Table 4b).

Flight Altitudes

The overall height distribution is given in Figure 5, and the associated mean and median altitudes were 1331 and 988 m, respectively (n = 1087). Migration was regularly

TABLE 4a. Proportion of eastward migration (30–150°) in different subsectors at different study sites.

Site no.	30–60° (%)	60–90° (%)	90–120° (%)	120–150° (%)	No. of tracks
1	0	3	75	22	73
2	7	21	24	48	29
3	3	38	55	3	29
4	0	6	66	28	104
5	0	44	53	3	64
6	0	0	87	13	55
7	8	23	49	20	152
8	9	30	31	30	70
9	9	32	49	10	79
10	2	24	71	2	41
Total 1–10	4	21	57	19	696
11–15	43	29	11	18	28

TABLE 4b. Proportion of westward migration (210–330°) in different subsectors at different study sites.

Site no.	210–240° (%)	240–270° (%)	270–300° (%)	300–330° (%)	No. of tracks
1–10	10	27	32	32	60
11	13	56	13	19	16
12	13	72	9	6	99
13	92	8	0	0	12
14–15	10	66	18	7	61

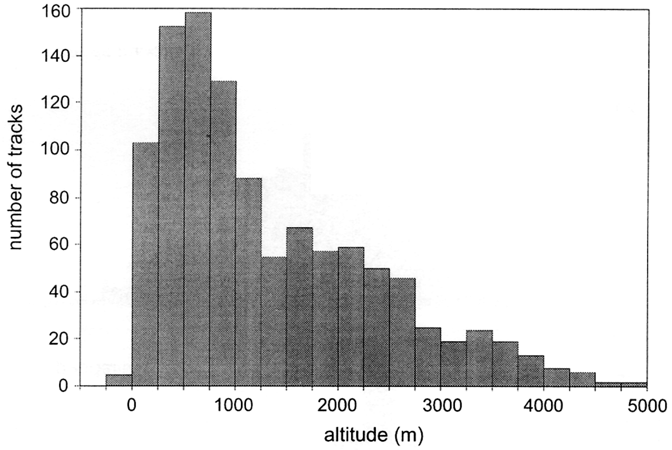

FIG. 5. Distribution of flight altitudes for the total sample of radar tracks (n = 1087) of migrating birds at the Northeast Passage. Altitudes refer to the height above the radar antenna, which was approximately 15 m above sea level.

recorded at very high altitudes, up to a maximum of 4816 m. The proportion of radar tracks in different height intervals fell with increasing altitude, from 50% at altitudes of 0–1 km, to 25% at 1–2 km, 17% at 2–3 km, 7% at 3–4 km, and 2% at 4–5 km. The occurrence of migration at the lowest end of the altitude spectrum must have been underestimated, because radar clutter often prevented the tracking of migrants at the lowest levels over the pack ice or sea.

Although ranges of altitudes were similar for E migration (30–150°) and W migration (210–330°), with top heights about 4800 m in both categories, E migration on average took place at higher altitudes than W migration. Median altitudes were 1337 m for E migration (n = 724) and 541 m for W migration (n = 248).

Speeds

Vertical speeds were usually close to zero, with an overall mean of 0.09 m/s (n = 882). The vast majority (75%) of vertical speeds fell in the range between -0.4 m/s and +0.4 m/s, which may be broadly regarded as level flight. The remaining cases consisted of 17% distinct climbing flights ($V_z > 0.4$ m/s) and 8% descending flights ($V_z < -0.4$ m/s). However, rates of climb or descent were mostly modest, and only 36 (4%) and 22 (2.5%) tracks may be classified as steep climbs ($V_z > 0.8$ m/s) or descents ($V_z < -0.8$ m/s), respectively. The steep climbs had vertical speeds up to 1.69 m/s, and most of them (27 of 36) were recorded at sites 7, 8, and 9, where the migrants gained height as they approached coastlines to the east and southeast. The median altitude of these steep climbs was 1076 m, and mean ground speed and airspeed were 16.9 m/s and 12.8 m/s, respectively. By comparison, the steep descents had vertical speeds between -0.8 m/s and -1.83 m/s, with an additional case of exceptionally steep rate of descent at -3.36 m/s. The median altitude for these descent flights was 697 m, and mean ground speed and airspeed were 17.3 m/s and 16.3 m/s, respectively.

Distributions of ground speed, airspeed, and wind speed are illustrated in Figure 6. Airspeeds fell in the range 8–20 m/s, with an additional tail (4%) of fast flyers with airspeeds exceeding 20 m/s. The overall mean airspeed was 13.8 m/s (SD = 3.0 m/s, n = 903). Ground speeds had a distinctly higher mean of 18.4 m/s and a much wider scatter (SD = 5.5 m/s, n = 1087). Ground speeds exceeded 20 m/s in 36% of all cases, and there was even a regular but sparse occurrence (2%) of ground speeds above 30 m/s up to a maximum of 37.7 m/s.

During their flights, the birds most frequently encountered wind forces up to 14 m/s, and the overall mean wind speed was 7.9 m/s (SD = 4.5 m/s, n = 903). However, there were also a remarkably large number of occasions (10%) when birds travelled in wind forces exceeding 14 m/s, with as many as 31 cases (3.4%) in winds of gale forces, between 18 and 24 m/s!

These flights in gale winds were recorded at Site 1 (5 July, n = 2), Site 7 (23 July, n = 8), Site 8 (31 July, n = 18) and Site 9 (3 August, n = 3). Winds were blowing from the west (220–285°) in all cases. Altitudes ranged between 510 and 2666 m (median 730 m), and the migrants were most often climbing (mean climb rate 0.28 m/s, SD = 0.36 m/s, max = 0.89 m/s). For 26 of the 31 cases, both track and heading directions were easterly (30–150°). Mean track direction was 73° and mean heading 93°, ground speeds were in the range 25.9–32.4 m/s (mean 28.6 m/s, SD = 1.7 m/s, n = 26), and airspeeds ranged from 8.4 to 14.8 m/s (mean 11.0 m/s, SD = 1.7 m/s, n = 26). The remaining five tracks did not constitute tailwind flights.

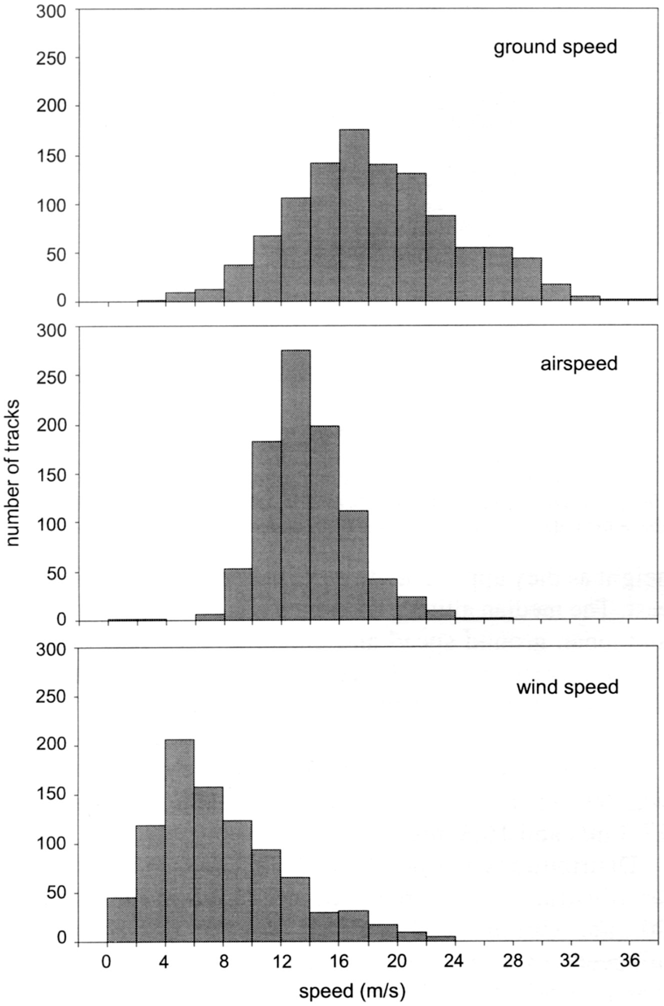

FIG. 6. Distributions of ground speed (n = 1087), airspeed (n = 903), and wind speed (n = 903) for the total sample of radar tracks of migrating birds at the Northeast Passage.

Four were crosswind flights (three tracks in northerly directions with WNW-NW headings and one easterly track with SSE heading), and one was a headwind flight (blown backwards from a heading/airspeed of 228°/16.2 m/s to a track/ground speed of 122°/5.9 m/s).

Wind is of primary importance for the flight economy of migrating birds, and the distribution of wind effect, defined as ground speed minus airspeed, is shown in Figure 7. The birds most often migrated in favourable winds that gave significant free gain in speed. The overall mean wind effect was +4.6 m/s (SD = 5.8 m/s, n = 903). In 80% of all cases, the birds benefited from the winds. In 16% of the cases, the wind effect exceeded +10 m/s, up to a maximum of +20.9 m/s.

E migration (30–150°) seemed to be relatively more favoured by winds than W migration (210–330°). In the former category, the wind effect was on average +5.8 m/s (SD = 5.4 m/s, n = 647); it was positive in 87% and exceeded +10 m/s in 19% of the cases. Mean ground speed of E migration was 19.6 m/s (SD = 5.3 m/s, n = 724), and mean airspeed was 13.5 m/s (SD = 2.7 m/s, n = 647). By comparison, the mean wind effect for W migration was only +1.6 m/s (SD = 5.9 m/s, n = 187). It was positive in 65% and exceeded +10 m/s in 10% of the cases. Mean ground speed of W migration was 16.2 m/s (SD = 5.2 m/s, n = 248), and mean airspeed was 15.0 m/s (SD = 3.3 m/s, n = 187).

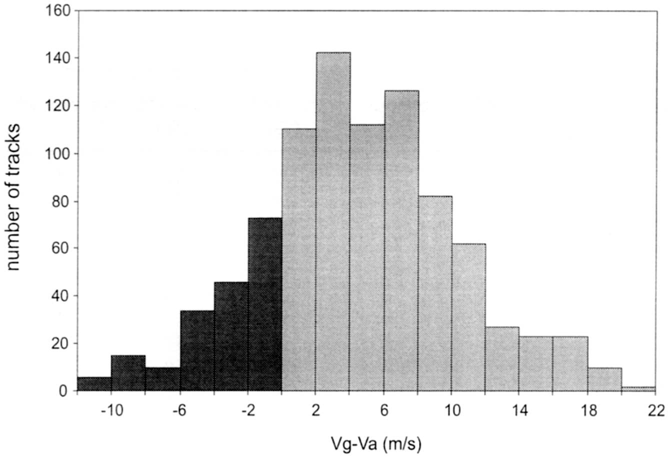

FIG. 7. Distribution of wind effect (ground speed minus airspeed) for the 903 radar tracks for which both ground speeds and airspeeds are available.

Flight Directions in Relation to Wind Compensation and Drift

The track vector (track direction/ground speed) of a flying bird is the sum of its heading vector (heading direction/airspeed) and the wind vector (direction/speed). The angle between track direction (T) and heading direction (H) may be regarded as either (1) an angle of compensation, if birds adjust their headings into the wind to maintain the same track irrespective of wind, or (2) an angle of drift, if they fly on constant headings and allow themselves to be drifted by the winds. In addition, there may be intermediate situations of partial compensation or drift, or responses like overcompensation (Alerstam, 1976, 1990; Richardson, 1991). The angle between track and heading directions, here denoted as α (= T-H), is positive when birds fly in winds with a cross component from the left and negative with winds from the right. One way of analyzing wind compensation/drift is to relate track and heading directions to the angle α as seen in Figure 8 (11 of the total 903 cases are not seen in this figure: with $|\alpha| > 60°$, they would fall outside the abscissa limits). Calculating the regressions of track and heading directions on α for a given cohort of migrants will give the regression equations:

$$T = D + b\alpha$$
$$H = D + (b-1)\alpha$$

where D is the intercept on the ordinate (flight direction when track and heading directions coincide, i.e., with no wind or due tail/headwinds) and b and (b-1) are the slopes of the two regressions. The coefficient b is expected to be 0 with complete wind compensation and 1 with full drift;

partial drift will be associated with values of b between 0 and 1, and overcompensation with negative values of b (cf. Alerstam, 1976).

We delimited two samples, of E migration (cases with $40^\circ \leq T \leq 160^\circ$ and $-30^\circ \leq \alpha \leq 30^\circ$, n = 590) and W migration ($210^\circ \leq T \leq 300^\circ$ and $-30^\circ \leq \alpha \leq 30^\circ$, n = 156) respectively, to calculate the above-mentioned regressions (cf. Fig. 8). For E migration, D was 103° (SE = 0.9° and 95% confidence interval 101–105°) and b was -0.02 (SE = 0.06; 95% confidence interval from -0.15 to +0.11). There was no correlation between T and α (r = 0.01), but a distinct negative correlation (r = -0.55) between H and α. For W migration, D was 258° (SE = 1.5°; 95% confidence interval 255–261°) and b was 0.05 (SE = 0.12; 95% confidence interval from -0.19 to + 0.29). Again, there was no correlation between T and α (r = 0.03) but a negative correlation (r = -0.54) between H and α.

The pattern emerging from these analyses is thus the same for both E and W migration. There is no tendency for the distribution of track directions to differ depending on if winds blow from the right or left, while there is a distinct shift of heading directions into the wind, to the same degree as expected with full compensation.

It is a remarkable coincidence of mirror-image symmetry that the mean directions D for E and W migration are 13° and 12° south of due east and due west, respectively.

Altitude Versus Directions and Speeds

Altitudes of the radar tracks are plotted in relation to track direction in Figure 9. A striking feature seen from Figure 9 is the substantial directional scatter at lower altitudes and the successively increasing concentration to the central sectors of E and W migration with increasing altitude. Above 3000 m, there is a very clearcut concentration of track directions in two relatively narrow sectors, 90–120° (E) and 250–270° (W).

Correlation coefficients between different speeds and altitude are given in Table 5. With the large number of available observations, even small correlation coefficients indicate statistically significant associations with $p < 0.05$ for correlation coefficients $r > 0.06$ and $p < 0.01$ for $r > 0.08$ for the data in Table 5. (It should be remembered that the fraction of variation accounted for is only r^2.)

There was a general tendency for both flight- and wind speeds to increase with increasing altitude. The wind effect, i.e., the increment in flight speed caused by wind (V_g - V_a), is shown in relation to altitude in Figure 10. While migration at low and moderately high altitudes involved cases of both positive and negative wind effects (with positive wind effects being predominant; cf. Fig. 7), flights at heights above 3000 m were almost exclusively associated with a positive wind effect. For the flocks that climbed above 4000 m, the gain in speed from the wind exceeded 10 m/s in most cases. However, the maximum gain from winds, 15–21 m/s, was attained by migrants flying with tailwinds of gale- or near-gale force at rather low and intermediate altitudes (cf. above).

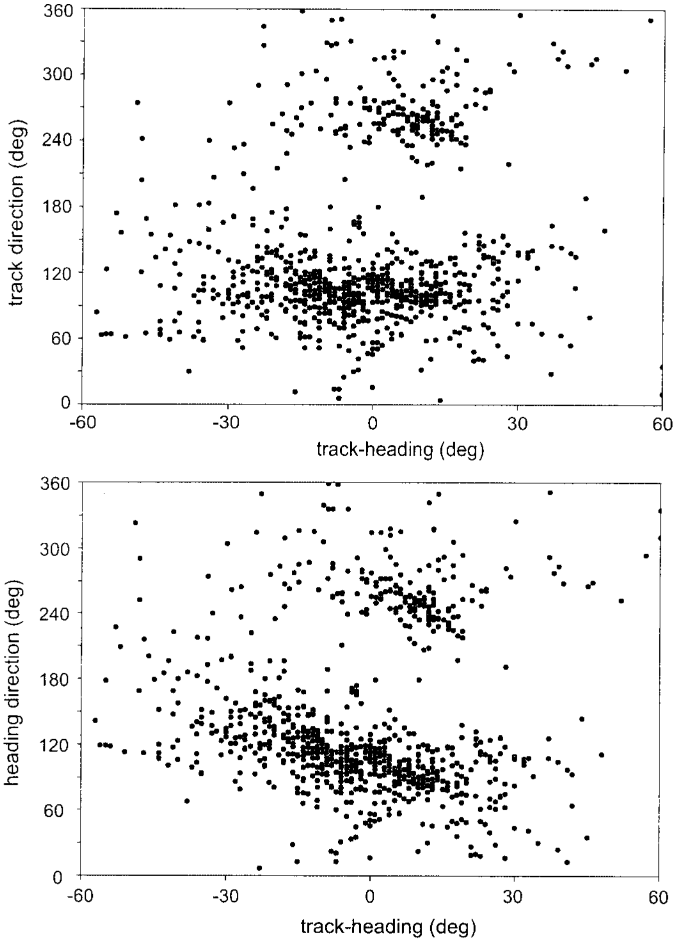

FIG. 8. Track direction (upper figure) and heading direction (lower figure) in relation to the angle between track and heading direction for the total sample of radar tracks for which both track and heading directions are available (n = 903, with 11 cases falling outside the abscissa limits in the figure).

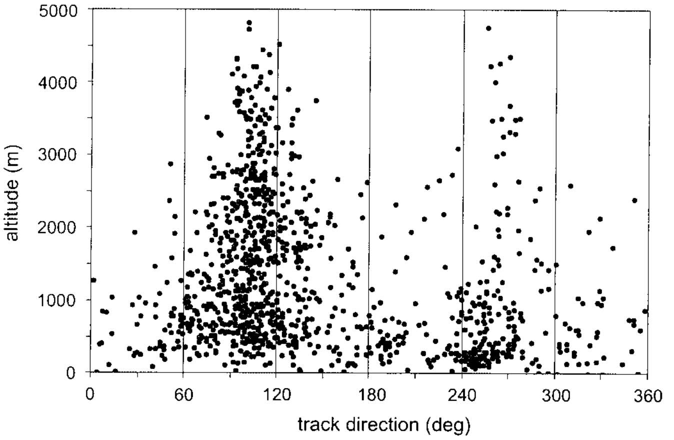

FIG. 9. Altitude in relation to track direction for the total sample of radar tracks (n = 1087).

Variation in Airspeed

Of course, the observed variation in airspeed reflects the fact that a variety of species with different characteristic ranges of flight speed are included in the radar data. But

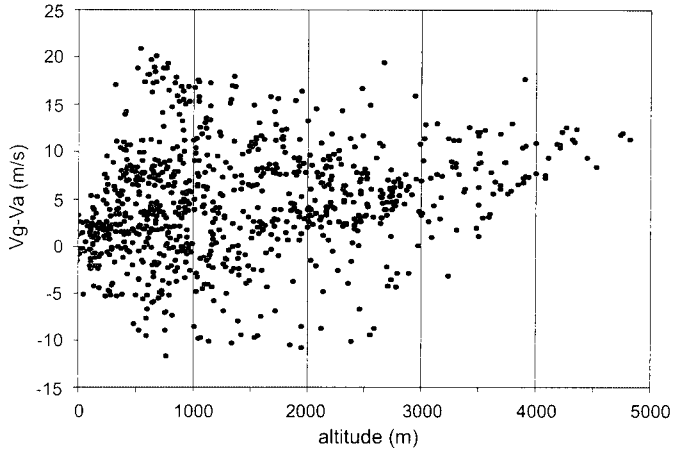

FIG. 10. Wind effect (ground speed minus airspeed) in relation to altitude for the 903 radar tracks for which both ground speeds and airspeeds are available.

TABLE 5. Correlation coefficients between different speeds and effect of wind on speed and altitude. V_a = airspeed, V_g = ground speed, $V_g - V_a$ = ground speed minus airspeed (wind effect), V_w = wind speed, V_z = vertical speed, and Z = altitude. No. of observations = 903 except as indicated.

	V_a	V_g	$V_g - V_a$	V_w	V_z	Z
V_a	1	0.17	-0.35	-0.06	-0.17[2]	0.05
V_g		1	0.87	0.64	0.06[1]	0.26
$V_g - V_a$			1	0.64	0.17[2]	0.22
V_w				1	0.19[2]	0.14
V_z					1	0.06[1]
Z						1

[1] No. of observations = 882.

[2] No. of observations = 734.

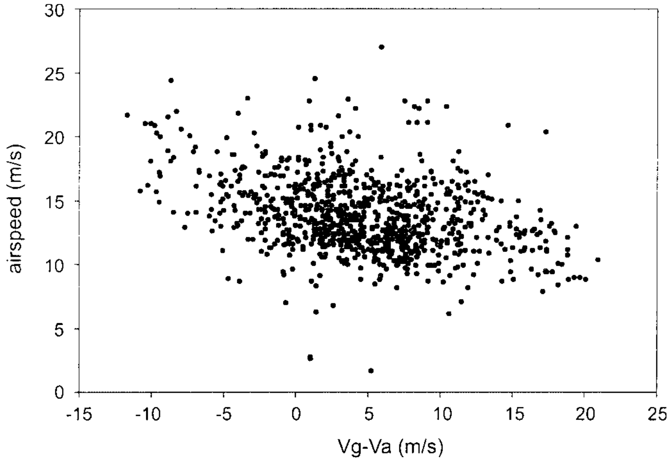

FIG. 11. Airspeed in relation to wind effect (ground speed minus airspeed) for the total sample of radar tracks where both ground speeds and airspeeds are available (n = 903).

this variation is also expected to be associated with changes in airspeed by individuals of any given species in relation to wind, altitude and rate of climb/descent (and to further variables like fuel load and flock size). According to flight mechanical theory one may predict a positive correlation between airspeed and altitude, and a negative correlation with wind effect and vertical speed (Pennycuick, 1975; Hedenström and Alerstam, 1995). Table 5 shows a distinct negative correlation between airspeed and wind effect (defined as $V_g - V_a$), and this relationship is plotted in Figure 11. Calculating the associated regression for airspeeds in the interval 8–20 m/s (airspeeds exceeding 20 m/s probably refer to a special category of fast-flying ducks; cf. above) gives the relationship:

$$V_a = 14.3 - 0.15\, X_1$$

where X_1 is the wind effect ($X_1 = V_g - V_a$, n = 856, r = -0.37, $p < 0.001$). Airspeed is predicted to vary not only with wind effect (defined as $V_g - V_a$), but also with the amount of compensation for crosswinds (Liechti et al., 1994). However, there was no significant correlation between airspeed and amount of compensation expressed as $1/\cos \alpha$ (calculated for cases with $|\alpha| < 60°$, n = 848, r = 0.025, $p > 0.05$; cf. Liechti et al., 1994), and neither was there any significant correlation with this variable after taking the wind effect into account.

In contrast, airspeed showed a significant association with vertical speed (V_z) as well as altitude (Z) after accounting for the wind effect. Together these three variables accounted for 20% of the variation of airspeed in the range 8–20 m/s, according to the following multiple regression equation:

$$V_a = 14.0 - 0.17X_1 - 0.84X_2 + 0.31X_3$$

where X_1 is the wind effect ($V_g - V_a$), X_2 is the vertical speed (V_z) and X_3 the altitude (Z) in km. The multiple correlation coefficient was 0.45 (n = 698), and the regression coefficients of all three variables were significantly different from zero ($p < 0.001$).

DISCUSSION

Migration Patterns

The two most distinctive features of the migration pattern along the Northeast Passage, as revealed in this study, are (a) the predominance and large-scale magnitude of migration in westerly (mainly 240–300°) and easterly (mainly 60–150°) directions and (b) the clearcut migratory divide between W migration, which dominates to the west of the Taymyr Peninsula, and E migration, which dominates to the east of Taymyr (cf. Table 4, Fig. 4).

The prevalence of E and W migration in the radar data is of course to a large degree a consequence of the positions of the study sites, at locations where any migration directed inland (southwards) from the coastal tundra would be out of reach. Only at sites 8, 9, 13, and 14 were there significant tundra areas to the north of the radar locations.

Sites 8 and 9 were at proper locations for recording southward departures from the New Siberian Islands, and there was indeed significant southward migration at Site 8, with tracks in the sector 150–210° making up 17% of the radar records at this site. In contrast, the corresponding S migration at Site 9 was minor, at 1%. Hence, even if substantial numbers of birds depart from the New Siberian Islands on southerly tracks, passages and departures in easterly directions are still much more numerous. At Site 13 on the west coast of Yamal Peninsula, migration was in the sector 174–246°, with two-thirds of all tracks towards S-SSW (174–210°). Thus, many birds from the Yamal Peninsula set out on courses across the Eurasian mainland rather than along the Arctic Ocean. At Site 14, 14% of the tracks were in the sector 160–200°, possibly reflecting southward migration from Novaya Zemlya.

These cases of southward departures from the New Siberian Islands, the Yamal Peninsula, and Novaya Zemlya indicate that there may be substantial southward migration of tundra birds departing across the Eurasian continent, out of reach of the observation sites in this study. We have no possibility of deciding about the relative quantitative importance of coastal and offshore E and W migration versus transcontinental southward movements in the total postbreeding exodus of waders and skuas from the tundra.

In the planning phase of our study, we were in fact contemplating the possibility that the overwhelming majority of tundra birds depart on southerly inland routes leaving only a trickle of movements to be encountered along the Northeast Passage north of the coast. However, our results have clearly refuted this possibility, demonstrating that E/W migration is by no means a marginal affair. Occasions of mass migration were repeatedly recorded with such an abundance of radar echoes (most of which of course had to be left untracked) that tens or hundreds of thousands of birds must have passed within the narrow radar range at these sites. In fact, many millions of birds of a variety of species must surely take part in the E and W migration at the Northeast Passage.

The ratio of W to E migration (number of tracks in W and E sector as in Fig. 4) shifted from 172:14 west of Taymyr (sites 12–14) to 60:696 east of Taymyr (sites 1–10), with Site 11 at the northern cape of this peninsula showing a rather even balance between the two directional cohorts. It is important to note that the migratory divide at Taymyr, although very prominent, does not involve a 100% directional shift. Relatively sparse but still clearly significant W migration was recorded at a number of sites in eastern Siberia.

Why does this divide coincide so neatly with the most northerly peninsula of the Eurasian continent? One important aspect is probably that this region around long. 100°E is almost exactly halfway between the Atlantic and Pacific "gateways" (the North/Norwegian/Baltic and Bering Sea regions, respectively) to the Eurasian High Arctic for birds migrating along W/E routes in the vicinity of the Northeast Passage. Hence, the divide may have evolved as a consequence of flight distance-dependent costs and competition effects between birds from different migratory populations according to principles illustrated by Alerstam et al. (1986) and Lundberg and Alerstam (1986).

Another possibility, although less likely, is that the geomagnetic field makes Taymyr a difficult and unfavourable region to migrate across (if birds orient by a magnetic compass). The geomagnetic field has it steepest inclination in this region, reaching 86° compared to other areas along the Northeast Passage where the inclination is between 78° and 84° (Peddie, 1993). Furthermore, within the Taymyr sector (long. 70–140°E), the magnetic declination (variation) changes with longitude in an opposite way compared to other sectors of the Northeast Passage (Peddie, 1993). This has the consequence that magnetic loxodromes (tracks with constant magnetic compass courses) curve unfavourably (prolonging flight distances) in the Taymyr sector, while they curve in a distance-saving way (compared to geographic loxodromes, i.e., tracks with constant geographic courses) on either side of this region. On the basis of spring arrival data for migratory birds in Russia, Middendorff (1855) already inferred the existence of a major divide between birds arriving from SW and W in European Russia and those arriving from SE and E in East Siberia. As the extrapolated main directions met right at the northernmost Taymyr Peninsula, Middendorff speculated that the birds were guided by a magnetic compass mechanism along directions converging on this site, which he (wrongly) thought was the location of the North Magnetic Pole.

Flight Routes in the Arctic Region

Since the birds migrating E/W along the Northeast Passage do not follow courses that point along geographic loxodromes directly towards their ultimate winter destinations, one may ask what are their intermediary destinations and passage areas in the arctic region? This is illuminated in Figures 12 and 13, where main directions of E and W migration, respectively, have been schematically represented on two different map projections: the Mercator and gnomonic projections (Gudmundsson and Alerstam, 1998b).

On the Mercator projection, the arrows indicate extrapolated flight routes if the birds maintain constant geographic courses and thus fly along loxodromes (which are shown as straight lines on a Mercator projection). On the gnomonic projection, in contrast, arrows indicate extrapolated flight routes along orthodromes (great circles, which appear as straight lines on a gnomonic projection).

If the birds maintain constant geographic courses, Figure12a indicates that the main stream of E-migrants (with track directions around 105°) will reach the coast of NW Alaska between Point Hope and Point Barrow. Lagoons along this stretch of coast attract large numbers of birds, among them shorebirds and terns on stopover during postbreeding migration (Johnson et al., 1993). However, the most important intertidal stopover habitats for waders are further south in Alaska, along the west and south coasts including the Alaska Peninsula (Gill and Handel, 1990;

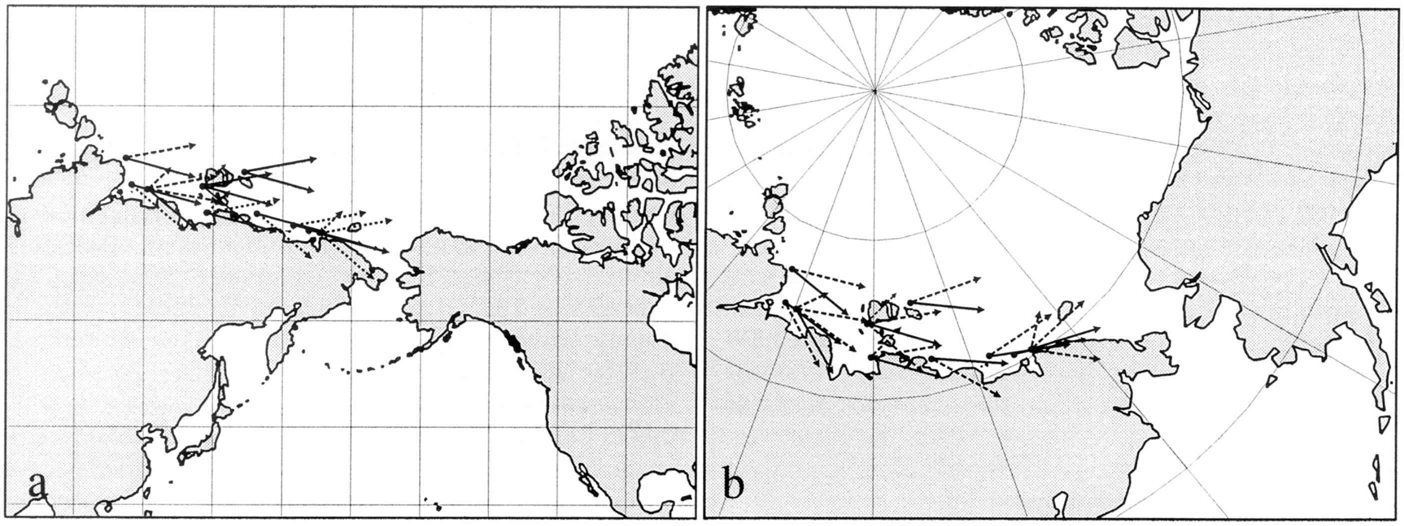

FIG. 12. Main directions of eastward migration plotted on two different map projections, the Mercator (a) and gnomonic (b) projections. The arrows are based on the information in Table 4a for Sites 1–10. Unbroken long arrows show the mid-direction of the dominating subsector (towards 105˚ for all sites except Site 2, where this direction is towards 135˚). Broken long arrows show mid-directions of subsectors with ≥ 20% of tracks. In addition, broken short arrows towards 45˚ are indicated for sites with a significant proportion of tracks (7–9%) in the northeasterly subsector (cf. Table 4a).

Gill and Senner, 1996; Piersma and Gill, 1998). Orthodrome-like routes would lead many Siberian migrants more directly towards these latter regions (Fig. 12b).

The scatter of E migration was substantial (Table 4a), and Figures 12a and 12b indicate that migrants with SE tracks fly across land of easternmost Siberia towards regions at the Bering Sea and the Sea of Okhotsk.

There was also important ENE migration (movements in the 60–90˚ sector comprised 21% of total E migration) and even NE migration (the fraction of tracks in the sector 30–60˚ approached 10% at a number of sites; cf. Table 4a). Loxodromic flight routes are quite unrealistic for these migrants, leading towards the Queen Elizabeth Islands in northernmost Canada or even north of Canada and Greenland, in a spiral towards the North Pole. We must assume that these migrants change their geographic bearings to the right during their flights across the Arctic Ocean, and if these changes are in accordance with those of orthodromes, the migrants will arrive in the Beaufort Sea region of Alaska and Canada on southeasterly tracks.

One possible interpretation is that E migration involves both loxodrome- and orthodrome-like routes. The Siberian north coast between Taymyr and Chukotka has an overall orientation about 100–110˚, and may provide topographical guidance for a loxodromic broad-front migratory ”highway” towards Bering Strait. This topographical guidance must act on a large scale (perhaps facilitated by the birds’ considerable flight altitudes), since the migrants generally maintained their courses irrespective of the highly indented structure of the coastline and the islands and promontories along the way. In contrast, birds departing ENE-NE across the Arctic Ocean (or SE across land) may follow more orthodrome-like routes.

Easterly high-altitude migration of birds arriving in Alaska from the west in July and August has been recorded by radars at Cape Prince of Wales (Bering Strait) and at the north coast (radars at Point Barrow, Oligtok, Barter Island) as reported by Flock (1972, 1973). One illustration in Flock (1972) from Cape Prince of Wales (24 July) shows tracks in the sector 110–160˚, with mean direction close to SE. An illustration in Flock (1973) from a north coast radar (at long. 150˚W on 2 August) shows both overland and offshore movements in the sector 90–100˚, i.e., parallel with the coastline. These high-altitude migrants were conjectured to be shorebirds that later headed south at the Mackenzie River; cf. Flock 1973). Spring migration towards W and WNW, most likely by shorebirds flying at high altitudes, was recorded by radars at the Yukon and Alaskan coasts of the Beaufort Sea (Richardson and Johnson, 1981). This migration may at least partly represent movements in the Siberian-American migration link with reverse spring directions, compared to the postbreeding migration in July and August.

The differences between loxodromic and orthodromic flight routes for W migration are illustrated in Figure13a and 13b. Extrapolating main direction (approx. 255˚) as loxodromes will point towards regions more northerly than the major passage and staging areas of arctic migrants in the Baltic Sea/North Sea/Wadden Sea regions (Smit and Piersma, 1989). Still, one cannot exclude the possibility that the mean orientation towards 250–260˚ at sites west of Site 11 (except Site 13) reflects the existence of a broad-front loxodromic highway in large-scale accordance with the overall alignment of the tundra coast, analogous to that discussed above for E migration at sites east of Taymyr. W migration in East Siberia was often directed WNW or even NW, which makes sense if the birds change courses in an orthodrome-like fashion (Fig. 13b) along routes leading towards the Atlantic or Mediterranean coasts of Europe.

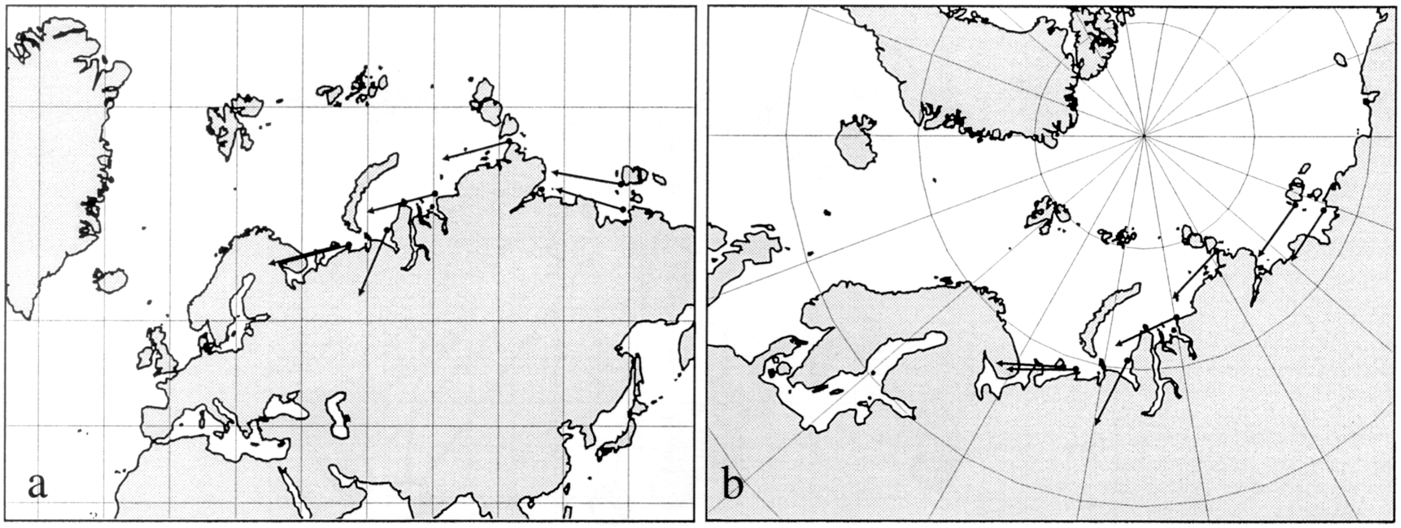

FIG. 13. Main directions of westward migration plotted on two different map projections, the Mercator (a) and gnomonic (b) projection. The arrows show the mid-direction of the dominating subsector (towards 255°) for Sites 11, 12, 14, and 15 according to Table 4b. For Site 13, the arrow shows the overall mean direction (203°), and for Sites 8 and 9, the arrows indicate the mean direction of westbound tracks (280° and 287°, respectively), according to Table 2.

Flight Routes on a Global Scale

Figure 14a-c illustrates Arctic flight routes in relation to the migrants' final winter destinations in a wider global perspective. Examples of departure locations on either side of the main W/E migratory divide (NW Taymyr and the New Siberian Islands, respectively) are connected with important winter destinations. Figure 14a is a Mercator projection, showing loxodromes as straight lines. Figures 14b and 14c are azimuthal equidistant projections; they show orthodromes from the centre as straight lines and give true distances and departure directions from the projection centre (Gudmundsson and Alerstam, 1998b). Information about migration routes and winter quarters for the species discussed below are based mainly on Cramp (1983), Higgins and Davies (1996), and del Hoyo et al. (1996).

The grey phalarope and pectoral sandpiper were prominent species among the eastbound migrants at several sites, often showing tendencies to depart on courses to the north of east. Their main winter destinations are in the Pacific Ocean off the coast of Chile (grey phalarope) and in South America, on the upland plateaus of Patagonia and up to 3500–4500 m in the Andes (pectoral sandpiper) (Fjeldså and Krabbe, 1990). Departure directions from the New Siberian Islands are approximately 60° (grey phalarope) and 36° (pectoral sandpiper) along orthodromes (Fig. 14b) and 145° and 138°, respectively, along loxodromes (Fig. 14a).

Palmén (1887) pointed out that the grey phalarope was the most abundant bird species encountered during the *Vega* expedition along the north coast of Siberia. It was repeatedly seen offshore in the pack ice. It was also among the few species recorded on several occasions during the summers of 1879–81 by the *Jeannette* expedition in the Arctic Ocean, far north of Wrangel Island (Vaughan, 1992). Grey phalaropes are known to concentrate during late summer at ice-edges well out in the Beaufort Sea north of Alaska (Johnson and Herter, 1989).

We conclude that many grey phalaropes probably depart E-ENE from Siberia on orthodrome-like routes across the Arctic Ocean towards the Beaufort Sea. Probably the majority cross the Arctic Ocean a bit to the south of the ideal orthodrome in Figure 14a and b. After a stopover in the Beaufort Sea, they may undertake a long-distance overland flight across western North America, in correspondence with the orthodrome (cf. below about arctic terns). But there is also evidence to suggest that many make a detour via the Bering Strait region, remaining over the ocean when continuing south along the East Pacific seaboard. Track directions of identified grey phalaropes (Table 3) indicate that some join the mainstream of eastbound migration towards ESE.

For pectoral sandpipers it has been suspected on the basis of their occurrence during migration that the main migration route actually follows close to a great circle towards South America (Hayman et al., 1986; Holmes and Pitelka, 1998). Many are known to migrate through the interior of the United States, especially during spring (Farmer and Wiens, 1998). On autumn migration, the passage across North America seems to be on a wide front. Many adults pass through inland regions, while juveniles disperse more widely to both the East Coast (flights across the western Atlantic were proposed by Hayman et al., 1986) and the West Coast (Paulson, 1993; Holmes and Pitelka, 1998). Siberian populations may connect with the migration system of the Nearctic populations, and the radar observations support the possibility of an orthodrome-like migration route, used by pectoral sandpipers that depart from Siberia in a first flight stage across the Arctic Ocean towards Alaska/N Canada. However, the radar data suggest that Siberian migrants seldom depart on such northerly bearings

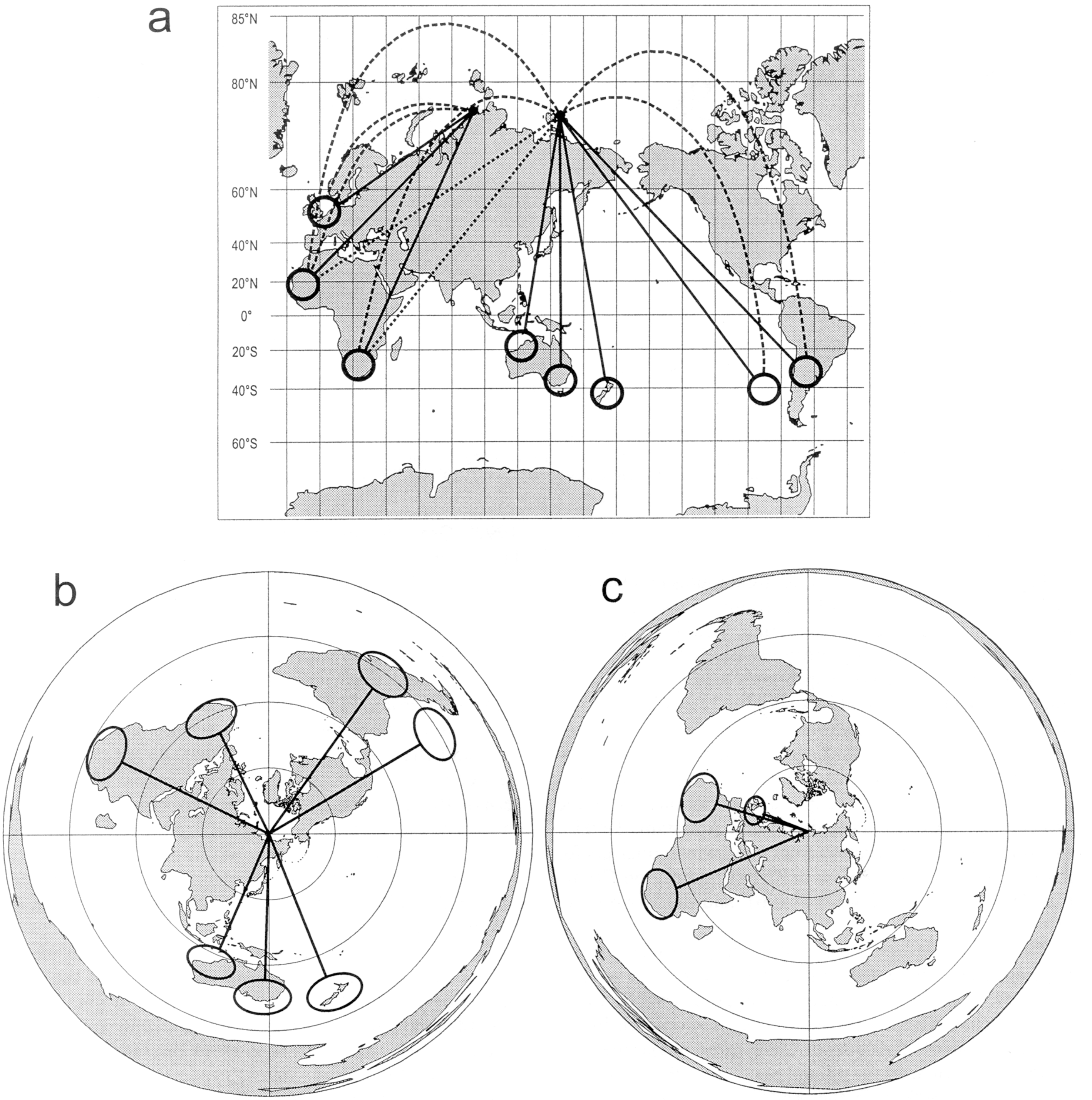

FIG. 14. Examples of important winter destinations for tundra birds breeding in NW Taymyr and the New Siberian Islands, with loxodromes and orthodromes (great circle routes) between breeding and wintering areas. (a) Mercator projection, showing the loxodromes as straight lines and the orthodromes as curved routes. (b) Azimuthal equidistant projection centered on the New Siberian Islands, showing orthodromes from this location as straight lines. (c) Azimuthal equidistant projection centered on NW Taymyr, showing orthodromes from this location as straight lines.

as 36° (departure direction of the ideal orthodrome from the New Siberian Islands for pectoral sandpipers) but more often towards E-ENE-NE along somewhat more southerly trajectories across the Arctic Ocean. Possible orientation principles based on celestial or geomagnetic cues that may guide the birds along flight routes across the Arctic Ocean between Siberia and North America have been analyzed in a separate paper (Alerstam and Gudmundsson, in press).

A number of further species may be involved in the Siberian-American migration link. The long-billed dowitcher has its winter quarters in the southern United States and in Central America. Among grey plovers (cf. Byrkjedal and Thompson, 1998) and sanderlings wintering along the western coasts of North and South America, there may well be birds of Siberian origin, and this is also very likely for pomarine skuas wintering in offshore

Pacific waters between California and Peru. Birds with these American destinations are expected to depart from Siberia on E-ENE bearings if they follow orthodrome-like routes (Fig. 14b). Another interesting species in this context is the arctic tern, which has winter quarters in the Antarctic pack ice zone. Large-scale migration is known from the Atlantic Ocean but also along the Pacific coast of South America (Salomonsen, 1967; Alerstam, 1985, 1990; Bourne and Casement, 1996). Villasenor and Phillips (1994) presented evidence in favour of an overland route across western North America to southwestern Mexico, whence the terns continue southwards over the eastern Pacific Ocean. It is likely that the terns normally complete this long-distance transcontinental crossing by nonstop flights at high altitudes and thus pass unnoticed by field observers. If there are Siberian arctic terns that connect with this route by travelling first across the Arctic Ocean to the Beaufort Sea, they will follow rather close to an ideal orthodrome towards southernmost South America, the Drake Passage, and Antarctica (Fig. 14b).

Many Siberian tundra birds have their main winter quarters in Australia and New Zealand. New Zealand harbours important winter populations of bar-tailed godwits, knots, and turnstones. Southeastern Australia is a destination of primary importance for curlew sandpipers and sharp-tailed sandpipers, as well as sanderlings, turnstones, and grey plovers. Northwestern Australia provides winter quarters for large numbers of bar-tailed godwits, knots, curlew sandpipers, and sharp-tailed sandpipers, with smaller but significant numbers of grey plovers, sanderlings, and turnstones. Recoveries from ringing and colour-marking demonstrate the Siberian origin of many of these winter visitors to Australia and New Zealand (Higgins and Davies, 1996). Catching and ringing birds during the "Tundra Ecology-94" expedition added further such evidence directly associated with our different study sites (Lindström et al., 1995; Alerstam and Jönsson, 1999). In addition to hosting waders, the Australian region is an important winter destination for pomarine skuas, which stay mainly well offshore, along the edge of the continental slope.

Loxodromes between the New Siberian Islands and the three main New Zealand/Australian areas in Figure 14 have bearings towards approximately 172°, 180°, and 191°, while the rather similar orthodromes have departure bearings from the New Siberian Islands at 157°, 180°, and 203°, respectively. These bearings are quite different from the dominating migratory direction towards ESE along the Northeast Passage in eastern Siberia.

Could it be that birds with winter destinations in New Zealand/Australia make a detour, first travelling E-SE to the Bering Sea region (to store fuel reserves) before turning southwest or south to migrate along the East Asian flyway or across the Pacific to their winter quarters? Such a pattern applies to the turnstone, according to evidence from extensive ringing and colour-marking of birds on stopover at the Pribilof Islands in the Bering Sea during postbreeding migration (Thompson, 1974; cf. Alerstam, 1990). Many turnstones using this stopover site originate from East Siberian breeding areas. They accumulate very large fuel reserves before departing S-SSW on extremely long flights across the central Pacific Ocean. They probably undertake nonstop flights as far south as the Marshall Islands or even further, and turnstones from Pribilof have been recovered on many Pacific islands all the way south to New Zealand and Australia.

Bar-tailed godwits using stopover sites at the Alaska Peninsula during postbreeding migration may represent a similar case. They store huge fuel loads and reduce their digestive organs before departing on long-distance transpacific flights, with New Zealand (also SE Australia) as a major winter destination (Piersma and Gill, 1998). There are speculations that they may cover the enormous distance to New Zealand more or less nonstop (Barter, 1989; Barter and Hou, 1990; Piersma and Gill, 1998). To what extent the bar-tailed godwits accumulating fuel in Alaska include birds from Siberia (and from how far in Siberia) is unknown (Gill and McCaffery, 1999). The populations staging in Alaska refer mainly to the subspecies *Limosa lapponica baueri* with breeding range in NW Alaska. The subspecies *L.l. menzbieri* has its main breeding distribution between the Lena and Kolyma Rivers in Siberia and its foremost winter quarters in NW Australia (Higgins and Davies, 1996; Engelmoer and Roselaar, 1998).

We conclude that the large-scale bird migration in the sector E-SE (with an overall mean direction about 105°) along the Northeast Passage east of Taymyr is composed of birds heading for the Bering Sea region. From there, they set out along the American or Asian coasts, or make transpacific flights, depending on their respective winter quarters. The flight to the Bering Sea region must represent a detour since there are no major winter quarters to be found along either orthodromes or loxodromes with bearings around 105° from northeast Siberia (Fig. 14). The reason for this detour is the rich marine and intertidal food resources of the Bering Sea region, which can be exploited for fuel deposition. In this way, the Bering Sea region represents a favourable "exit gateway" for many shorebirds (not only turnstones and bar-tailed godwits), skuas and terns from the Siberian coastal tundra.

For westbound migration of arctic waders from NW Taymyr to major winter quarters in W Europe (e.g., dunlin and bar-tailed godwit), W Africa (e.g., knot, curlew sandpiper, bar-tailed godwit, little stint, sanderling, and ruff), and southern Africa (e.g., knot, curlew sandpiper, little stint, ruff; cf. Smit and Piersma, 1989), the departure directions are approximately 237°, 226°, and 206° for loxodromes and 293°, 287°, and 248° for orthodromes (Fig. 14a, c). Courses along loxodromes and orthodromes for pomarine skuas and grey phalaropes that winter in the Atlantic off the W African coast are similar to those toward Europe and W Africa, but slightly more to the west or northwest.

Recoveries of ringed birds have suggested an orthodrome-like route between the tundra and South Africa for curlew sandpiper, little stint, and ruff (Elliott et al., 1976; Summers and Waltner, 1978; see also Dick et al., 1976). The overall mean direction of westbound migration (about 255°, according to the radar results from sites west of Taymyr) suggests a trajectory towards W Europe/W Africa that falls in between the ideal loxodromes and orthodromes, respectively. The reason may be that the main migratory highway towards these destinations is to some extent influenced by large-scale topography, running parallel with the tundra coast and in association with the White Sea, the Baltic Sea, and the Atlantic seaboard in W Europe.

The ruff is one of the most important candidate species for regular westbound migration all the way from eastern Siberia towards the main wintering regions in western and southern Africa (cf. Alerstam, 1990). Departure bearings along orthodromes from the New Siberian Islands to western and southern Africa are approximately 336° and 298°, respectively (Fig. 14b), while the corresponding loxodromes have courses at 237° and 220°, respectively (Fig. 14a). The fact that westbound migration east of Taymyr was directed mainly in the sector W-NW (Table 4b) supports the possibility of orthodrome-like migration routes towards these destinations, although departure directions had a smaller northerly component than expected for ideal orthodromes.

Our general conclusion is that the radar data from the Northeast Passage, when interpreted in a global perspective, indicate elements of both orthodrome- and loxodrome-like routes and of large-scale topographic guidance in the migratory pathways of tundra birds. The birds must have a course-control system that is versatile enough to permit orientation along routes in broad resemblance with great circles (Alerstam and Pettersson, 1991), but also in broad harmony with large-scale topographic features and along trajectories involving sharply defined detours. In addition, it should be remembered that autumn and spring migration routes are often different (loop migration).

Flight Performance and Strategies – Compensation for Wind Drift

If winds vary between different segments of the migratory journey, birds may benefit from a strategy of minimizing the distance to the final destination after each flight. This strategy implies adapted drift, e.g., the birds expose themselves to extensive wind drift on flights far away from the goal and compensate for the wind drift to a greater and greater degree the closer they get to the final destination (Alerstam, 1979). In addition, a bird should coordinate this general pattern of adapted drift with changes in airspeed to obtain the optimal heading vectors for completing the entire migratory journey at minimum energy cost (Liechti, 1995).

The tundra birds recorded in this study had just started their postbreeding migration and were very far away from their final winter destination. Contrary to expectation for birds using a strategy of adapted drift, complete compensation for wind drift was the prevailing pattern for both east- and westbound migration. Why would the tundra birds not allow themselves to be wind-drifted, if this behaviour would allow them to approach their winter destinations more efficiently?

An important disadvantage of adapted drift (or any strategy involving tolerance of wind drift) is that the exact route to the destination becomes unpredictable (Alerstam, 1979, 1990; Richardson, 1991). Hence, the birds will have to use different stopover sites depending on where the winds happen to carry them, and they may be wind-drifted over inhospitable areas. It could well be that suitable stopover habitats for the tundra birds are restricted to specific sites and regions, from which the migrants cannot afford to deflect. If migrants depend on such specific stopover sites or regions, these will correspond to goals to the same extent as the final winter destination, and the birds will be expected to approach these intermediary goals by flights involving compensation for wind drift. For the many migrants travelling in broad correspondence with the tundra coast along the Northeast Passage, the coastal region may offer suitable stopover and landing sites, and at the same time provide visual reference cues that facilitate compensation for wind drift.

The basic pattern of complete compensation for wind drift seems to apply also to migrants departing from Siberia in the sector 30–90° across the Arctic Ocean towards North America (cf. Fig. 8). For these migrants, any tolerance of wind drift may be counter-selected because of the risks of drift towards the central Polar Basin or towards barren polar land.

Risks Associated with Strong Wind Forces

Wind speeds that exceed the birds' airspeed circumscribe the birds' possibilities of orientation. The range of possible track directions becomes restricted within $\pm\beta°$ from the downwind direction according to the relationship:

$$\beta = \arcsin (V_a/V_w)$$

where V_a is airspeed and V_w is wind speed (Alerstam, 1978).

Remarkably often, the tundra birds were migrating in strong winds: cases with wind speed exceeding airspeed made up 12% of the total sample. In more than 3% of the cases, the birds travelled in winds of gale force, between 18 and 24 m/s. With a typical airspeed about 14 m/s, the scope of orientation in these latter situations was restricted within ± 51° and ± 36°, respectively, from the downwind direction. There were even a number of cases (n = 13; 1.5%) with wind speed more than twice as high as the airspeed, giving values of β smaller than 30°.

The birds may, if necessary, alleviate part of this restriction by increasing their airspeed, but it may be difficult or even impossible for them to overpower gale-force winds for longer periods of time. Hence, the advantage of very strong tailwinds for obtaining a fast ground speed and low transport cost is counteracted by increased risks of unavoidable drift (if wind direction changes during the flight) and of losing the security associated with the possibility of making return flights.

We have the impression that intensive bird migration in such very strong wind forces as recorded in this study is unusual. Could it be that the tundra birds including the category flying across the Arctic Ocean in the Siberian-American migration link, are more risk-prone than migrants in many other situations? Do they give priority to a swift and energy-efficient departure at the cost of the high risk level associated with the strongest tailwinds? Such risk proneness may be associated with time-selected migration, when the migrants have much to gain by arriving early, before their competitors, at critical stopover sites as well as at the final winter destination.

Altitudes

The tundra migrants were often flying at high altitudes (Fig. 5). Similar or even higher altitudes have been recorded by radar for long-distance shorebird migration over Nova Scotia and New Brunswick in autumn (Richardson, 1979). These latter shorebirds, departing towards the southeast over the Atlantic Ocean, flew at a median altitude of 1.7 km, with 25% of the recorded flocks above 3 km, 10% above 4 km and a highest altitude of 6.65 km. These figures may be compared with the corresponding figures for the tundra migrants: a median altitude of 1.0 km, 9% above 3 km, 2% above 4 km and a top height of 4.8 km. The mean ground speed of the shorebirds departing over the Atlantic was 20.6 m/s (SD = 4.7 m/s), which is slightly faster than the overall mean of 18.4 m/s (SD = 5.5 m/s) for the tundra birds in this study. The main reason for the fast ground speeds in both studies are (1) the birds' distinct preference of occasions with following winds for their flights and (2) their capacity to climb to very high altitudes in situations when the tailwind assistance increases with altitude (Fig. 7).

Variation in Airspeed

The overall distribution of airspeeds (Fig. 6) as well as the airspeeds of identified species and groups (Table 3) may be compared with speeds predicted from flight mechanical theory, as given for a sample of species in Table 6. Body mass and wing measurements are derived mainly from Hedenström (1995), with complementary data from Greenewalt (1962) and Lindström (1998). Total body masses are based on the assumption that the tundra migrants fly with rather modest fuel loads. Aspect ratio, which is calculated as b^2/S (where b = wing span and S = wing area), is a measure of wing shape, corresponding to the mean ratio of wing length to chord. The airspeeds for minimum power (V_{mp}) and maximum range (V_{mr}) have been calculated according to Pennycuick (1975, 1989), with modified assumptions about profile power ratio (= 9.4/AR, where AR is aspect ratio; Pennycuick, 1995) and about coefficient of body drag (= 0.1; Pennycuick et al., 1996).

The calculated speeds are to be regarded as highly provisional estimates, because of uncertainties in the assumptions about the aerodynamics of flapping flight. V_{mp} is the speed where power is at its minimum, while V_{mr} is the speed where the ratio of power to speed (which is equivalent to energy cost per unit of distance covered) is minimal. This latter speed will allow a bird to cover the maximum range on a given fuel load. In time-selected migration, where birds minimize the resulting speed of migration, they are expected to fly faster than V_{mr} to an extent that depends on the energy accumulation rate during fuel deposition periods (Alerstam and Lindström, 1990).

For the waders, skuas, and terns in Table 6, predicted values of V_{mp} fall in the range 7–12 m/s, and the corresponding range for predicted V_{mr} is 13–19 m/s. Only a minority of observed airspeeds (26%), at the lower end of the distribution, fall in the range predicted for V_{mp} (Fig. 6). There is better agreement with predicted V_{mr}, although the above-mentioned proportion of slow airspeeds is difficult to reconcile with this speed (see below about effect of wind on V_{mr}). The data for identified waders, skuas, and terns in Table 3 show airspeeds that are intermediate between V_{mp} and V_{mr}, most often closer to V_{mr} than to V_{mp}. Steller's eiders and long-tailed ducks, which have very similar size and measurements and thus very similar predicted speeds, account for the airspeeds above 20 m/s (cf. Table 3). This is in reasonable accordance with predicted V_{mr} (Table 6), although again on the low side.

Flight speeds are expected to increase with altitude, because of the effect of air density on the balance between flight power components (Pennycuick, 1975). Both V_{mp} and V_{mr} are expected to increase by about 5% per 1 km increase in altitude (calculated on the basis of the reduction of air density with altitude in the standard atmosphere). With a mean airspeed of 14 m/s, this implies an increase of about 0.7 m/s per km in altitude. The observed airspeed was indeed positively correlated with altitude, but the increase in speed with altitude (regression coefficient 0.31) was only about half of that expected.

V_{mp} remains the same irrespective of wind, whereas V_{mr} is dependent on wind, being faster in opposing winds than in following winds (Pennycuick, 1975). We calculated the expected change in V_{mr} in relation to wind effect (ground speed minus airspeed) for the species in Table 6. Although this relationship is not strictly linear (cf. Liechti et al., 1994), the expected slope (in the wind-effect interval -8 to +12 m/s) is approximately -0.35. Observed airspeed did vary significantly with wind effect (Fig. 11, Table 5), indicating that the birds did not fly at any fixed V_{mp}. However, the slope of this relationship (regression coefficient of -0.15 or -0.17) was less steep than predicted for V_{mr}. Airspeed also showed a significant correlation with vertical speed, which is in line with findings for migrating terns and waders elsewhere (Alerstam, 1985; Piersma et al., 1997).

TABLE 6. Airspeeds for minimum power (V_{mp}) and maximum range (V_{mr}) as calculated from flight mechanical theory on the basis of the body measurements given for a sample of tundra migrants. Calculations refer to flight at low altitude (air density 1.23 kg/m^3) and in calm or neutral winds (see text about effects of altitude and wind).

Species	Body mass (kg)	Wing span (m)	Wing area (m^2)	Aspect ratio	V_{mp} (m/s)	V_{mr} (m/s)
Brent goose	1.35	1.20	0.146	9.9	14.3	22.4
Long-tailed duck	0.80	0.70	0.060	8.2	15.7	25.2
Little stint	0.024	0.31	0.0113	8.5	7.3	12.7
Dunlin	0.053	0.37	0.0165	8.3	8.7	14.8
Grey phalarope	0.060	0.42	0.0196	9.0	8.5	14.3
Knot	0.15	0.52	0.0286	9.5	10.4	16.8
Ruff	0.17	0.58	0.0417	8.1	10.2	17.1
Grey plover	0.26	0.63	0.0437	9.1	11.4	18.3
Bar-tailed godwit	0.32	0.73	0.0608	8.8	11.3	18.3
Pomarine skua	0.75	1.18	0.139	10.0	11.8	18.8
Arctic tern	0.13	0.80	0.0571	11.2	8.0	13.3

We conclude that the tundra migrants generally fly faster than V_{mp} and that they adjust their airspeed in qualitative agreement with expectations for V_{mr}. However, the observed airspeeds seem most often to fall below predicted V_{mr}. There is no obvious reason why the migrants would fly slower than V_{mr}, wasting energy as well as time, unless they have insufficient muscle power to maintain this speed or muscle efficiency changes with speed (cf. Thomas and Hedenström, 1998). Of course, it may also be that the values of V_{mr} in Table 6 are overestimates. One reason to suspect this is the assumption that profile power is independent of speed, which cannot be true at high speeds (Tucker, 1973; Pennycuick, 1989; Alerstam, 1999).

Wind and Range

It is hardly possible to overestimate the importance of wind for the flight economy and range of migrating birds. The tundra birds took advantage of following winds to an impressively high degree (Fig. 7). The average wind gain of + 4.6 m/s is larger than that recorded by Gudmundsson (1993) for spring migration of waders and geese in Iceland (about + 2 m/s), but somewhat smaller than the gain he recorded for knots on spring migration across Scandinavia (about + 7 m/s; Gudmundsson, 1994). Examples of further evaluations of the importance of winds for migrating shorebirds are those by Piersma and Van de Sant (1992) and Butler et al. (1997).

Little is known about the quantity of fuel reserves the tundra birds store before departing on their postbreeding migration. Many adult waders typically forage at tundra pools before departing in July, when there is still ice along the coasts. Littoral habitats become available for exploitation on a large scale in August, not least by the large numbers of juvenile waders departing at this time. At least for the first wave of departing adult birds, the time interval between breeding and departure from the tundra is so short that it is uncertain whether they have had time to increase their body mass much beyond that recorded during breeding (Hedenström, 1995). Still, with a fuel load as modest as 20% (ratio of fat load to lean body mass) waders may travel 2000 km in still air, and as far as 2700 km with average wind assistance (+ 4.6 m/s), calculating on the basis of Pennycuick (1989) and Gudmundsson et al. (1991), with modified assumptions as described in the preceding section. This means that such modest departure fuel loads are probably sufficient even for the birds making direct flights across the Arctic Ocean between Siberia and America (Fig. 14).

Lindström (1998) demonstrated that juvenile little stints store only relatively small fuel loads, 12–19%, at the tundra coasts of the Northeast Passage in August. It was only at the westernmost sites that they built up heavier fuel loads, corresponding to 25–40% of lean body mass (Lindström, 1998).

It remains to be investigated whether it is a typical pattern for migrants not to store larger fuel loads until they reach the entrances to the North Atlantic and Pacific Oceans. With fuel loads of 50–100% in combination with a fair amount of wind assistance, the birds' potential flight ranges may reach amazing magnitudes, between 4000 and 9000 km. Further knowledge about the birds' fuel deposition when leaving the tundra and High Arctic habitats will be of greatest importance for our understanding of the departure strategies of these migrants.

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