Orientation, Migration Routes and Flight Behaviour of Knots, Turnstones and Brant Geese Departing from Iceland in Spring

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ABSTRACT. Flight behaviour and orientation of 303 flocks (31 200 individuals) of migrating Knots and Turnstones and 77 flocks (3200 individuals) of Brant Geese departing from Iceland towards Nearctic breeding grounds were recorded during three spring seasons 1986-88. Flocks were tracked by telescope and optical range finder at three observation sites in western Iceland during the peak period of migratory departure, 25 May-1 June. Departing waders climbed steeply, often by circling and soaring flight, with an average climbing rate of 1.0 m·s⁻¹, up to altitudes 600-2000 m asl. With unfavourable winds, the waders descended to fly low over the sea surface. Brant Geese usually travelled at lower altitudes, the majority below 100 m above the sea, and were more prone towards following coastlines than waders. The birds departed in flight formations, with mean flock sizes 100-200 individuals in the Knot, 13-70 individuals in the Turnstone and about 40 individuals in the Brant Goose flocks. Waders generally departed in the afternoon or evening, during rising or high tide. Significant differences in daily timing between seasons were associated with between-year differences in the tidal cycle. Within the season, departures took place earlier in relation to high tide as the season progressed. Brant Goose departures occurred in the morning and late evening.

Mean orientation was close to 300° in all three species, with angular deviation 21-26°. It is concluded that the overwhelming majority of the birds are bound for breeding sites in northern Canada and northwest Greenland. The main flight route, as can be deduced on the basis of visual, radar and ringing data from Iceland, Greenland and Canada, falls in the 290-310° rhumbline sector from Iceland, across the Greenland ice cap. There are simple celestial and magnetic orientation rules that would allow birds to orient from Iceland to northern Canada close to a great circle route, but not along the rhumbline route used by the Knots, Turnstones and Brant Geese.

Key words: bird migration, orientation, timing, flight behaviour, flocking, Calidris canutus, Arenaria interpres, Branta bernicla, Iceland

RÉSUMÉ. Au cours des trois printemps de 1986 à 1988, on a procédé à des relevés du comportement et de l'orientation en vol durant la migration de 303 volées (31 200 individus) de bécasseaux maubèches et de tourne-pierres à poitrine noire, ainsi que de 77 volées (3200 individus) de bernaches cravants, qui avaient quitté l'Islande pour des aires de reproduction dans le Néarctique. On a suivi la trajectoire des volées en se servant de télescopes et de télémètres optiques à trois endroits dans l'ouest de l'Islande, au cours de la période de pointe du départ pour la migration, soit du 25 mai au 1ᵉʳ juin. Lorsqu'ils partaient, les échassiers s'élevaient rapidement en décrivant souvent des cercles et en s'élançant vers le ciel, la moyenne de leur taux d'ascension étant de 1,0 m·s⁻¹. Ils atteignaient des altitudes de 600 à 2000 m au-dessus du niveau de la mer. Lorsque les vents étaient contraires, ils redescendaient pour voler plus près de la surface de l'eau. Les bernaches cravants voyageaient d'ordinaire à des altitudes plus basses — la majorité à moins de 100 m au-dessus de la surface —, et elles avaient plus tendance à suivre les côtes que les échassiers. Lors de leur départ, les oiseaux étaient en formation de vol et la taille moyenne des volées était de 100 à 200 individus pour les bécasseaux maubèches, de 13 à 70 individus pour les tourne-pierres à poitrine noire et d'environ 40 individus pour les bernaches cravants. En général, le départ des échassiers avait lieu l'après-midi ou dans la soirée, à marée montante ou à marée haute. Des différences significatives dans l'horaire quotidien d'un printemps à l'autre, étaient associées aux différences présentes d'une année à l'autre dans le cycle des marées. Au fur et à mesure que la saison avançait, le départ se faisait de plus en plus tôt, par rapport à l'heure de la marée haute. Le départ des bernaches cravants avait lieu le matin et tard le soir.

L'orientation moyenne était proche de 300° pour les trois espèces, avec une déviation angulaire de 21 à 26°. On en conclut que la grande majorité des oiseaux se dirigent vers des aires de reproduction situées dans le nord du Canada et le nord-ouest du Groenland. La trajectoire principale du vol, que l'on peut déduire des données obtenues par observations visuelles, par radar et par le baguage des oiseaux, en Islande, au Groenland et au Canada, se situe dans le secteur loxodromique de l'Islande de 290 à 310° à travers la calotte glaciaire du Groenland. Il existe des règles simples d'orientation céleste et magnétique qui permettraient aux oiseaux de s'orienter depuis l'Islande jusqu'au nord du Canada en suivant un grand cercle, mais pas le long de la route loxodromique qu'empruntent les bécasseaux maubèches, les tourne-pierres à poitrine noire et les bernaches cravants.

Mots clés: migration, orientation, époque, comportement en vol, volée, Calidris canutus, Arenaria interpres, Branta bernicla, Islande

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INTRODUCTION

High Arctic birds show complex migration patterns, with several alternative spring staging sites and flight routes to their destinations. Iceland serves as the most important entranceway to Nearctic breeding regions for different species of waders and geese wintering in western Europe. Large proportions of the western European wintering populations of the Knot *Calidris canutus islandica* (total population about 350 000 individuals; Prater, 1981), Turnstone *Arenaria interpres* (provisional population estimate about 50 000 individuals; Prater, 1981) and Light-bellied Brant Goose *Branta bernicla hrota* (about 20 000 individuals; Salmon *et al.*, 1988) make a stop during most of May in Iceland, where the birds accumulate large amounts of fat before their final long-distance flights to the Nearctic breeding grounds (Nielsen, 1918-19; Timmermann, 1938-49; Salomonsen, 1950, 1967; Morrison, 1977; Wilson, 1981).

However, not all birds of the above-mentioned populations travel via Iceland in spring. Considerable numbers of Turnstones apparently depart towards Nearctic breeding grounds directly from Britain and Ireland (Clapham, 1979; Prater, 1981), while Knots and possibly Brant Geese migrate via Norway (Davidson *et al.*, 1986; Hjort *et al.*, 1987).

It was originally believed that Knots, Turnstones and Brant Geese staging in Iceland during spring were all destined for breeding grounds in NE/N Greenland (Timmermann, 1938-49). However, visual observations, ringing results and radar records have since corroborated the conclusion by Salomonsen (1950, 1967, 1979) that there exists an important flyway from Iceland to northern Canada/northwest Greenland across the Greenland inland ice (Morrison, 1975, 1977; Maltby-Prevett *et al.*, 1975; Wilson, 1981; Alerstam *et al.*, 1986).

It remains to be clarified if there is any difference in the relative importance of Iceland as a spring staging area for

birds breeding in NE/N Greenland and N Canada/NW Greenland respectively. This is important for mapping the European-Nearctic migration system and for judging which selective factors related to flight distances, weather en route, orientation conditions, timing of migration, competition and predation may affect the evolution of arctic migration systems (Morrison, 1984; Alerstam et al., 1986; Uttley et al., 1987).

The flight between Iceland and N Canada is of unique interest from the point of view of bird orientation and navigation. At northerly geographic and magnetic latitudes the birds are faced with difficulties in using the sun compass (problems of time compensation during rapid longitudinal displacement), star compass (not visible with 24 h daylight) and magnetic compass (an excessive declination and inclination makes the geomagnetic field unreliable for orientation purposes within a wide region around the north magnetic pole). Hence, flight directions and behaviour of migrants departing from Iceland may, in conjunction with radar records of spring migration across the Greenland inland ice (Alerstam et al., 1986), provide important clues about the precise trajectory of the main flight route and orientation premises.

In this paper we present and analyze the orientation, timing and behaviour of Nearctic Knots, Turnstones and Brant Geese departing from Iceland in late May and early June. Our aim is primarily to throw light on the main questions raised above: How do the migrants staging in Iceland distribute themselves with respect to the two different main destination areas, in NE/N Greenland and N Canada/NW Greenland, and what may be the reasons for the pattern observed? Along which route do the migrants fly from Iceland to N Canada, and can we infer from the trajectory and from the birds' behaviour how they orient at these northerly latitudes?

OBSERVATION SITES AND METHODS

Systematic observations of migrating birds were carried out during the period of peak departure, 25 May to 1 June, in three years, 1986-88. Observations were conducted at three different sites (Fig. 1):

Malarrif (64°44'N, 23°48'W): A team of three resident observers kept constant watches generally 07-11 h (local Icelandic time = GMT) and 18-23/24 h each day during the study period in 1986. Additional observations were made outside the above-mentioned periods when migrating birds appeared. The observation site at the shoreline at Malarrif lighthouse on the south coast of Snaefellsnes peninsula offered an unobstructed view along the coast towards the east and west-northwest and over the open sea in the sector in between. The Snaefell mountain and its ice cap (1446 m asl) rise about 8 km to the north of the observation site.

Latrabjarg (65°30'N, 24°32'W): Observations were carried out from the westernmost tip of Iceland, at the Bjargtangar lighthouse (31 m asl), by two observers in 1986 during the same morning and evening periods as at Malarrif. A few additional records of migrating flocks were made during a visit to this site in the afternoon and evening 31 May 1988. Huge numbers of seabirds breed at the Latrabjarg cliff, which extends 12 km eastward from the observation site, rising to 440 m asl.

Vatnsfjördur (65°35'N, 23°10'W): A team of three or four observers kept constant daily watches for migrating birds between 15.00 and 23.00 h in 1987 and 1988. During both
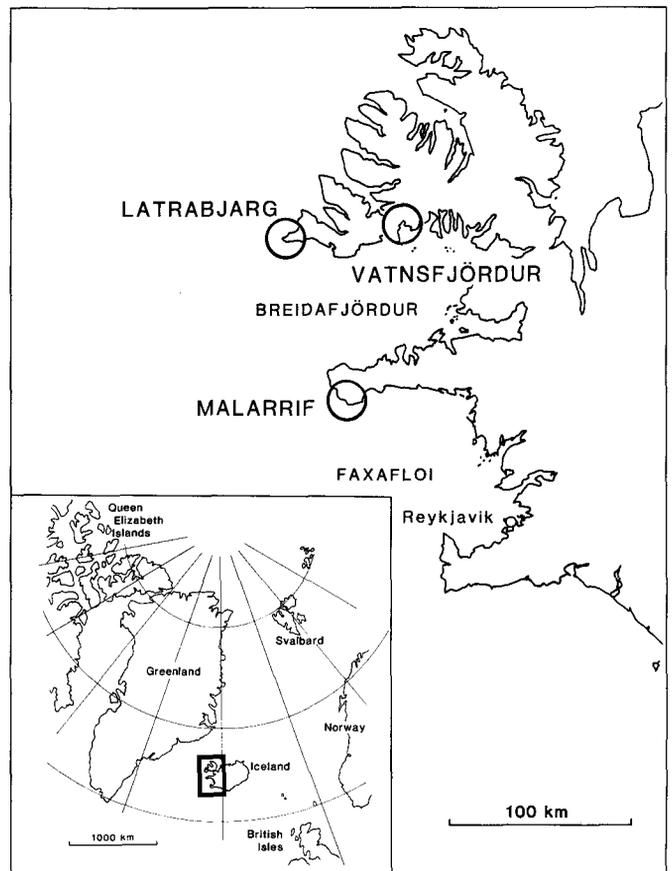
FIG. 1. Location of the three main observation sites (encircled) on the west coast of Iceland.

years, four or five observers stayed at this site and carried out field work at all times during the day. However, we failed to record any significant migration outside the hours of regular watch. Observations were carried out from both the western and eastern shores of the fjord. The highest peak in the vicinity reaches 747 m asl, about 8 km to the northwest. Additional records of a few departing wader flocks during a visit at this site on 1 June 1986 are also included.

Migrating flocks were normally located by using 10× binoculars and later tracked in 20-22× telescopes until they vanished from sight. Telescopes were equipped with azimuth and elevation scales and were carefully aligned to give geographic compass bearings and elevation angles. The following data were recorded in order to determine flight directions of the birds: (1) the compass bearing (= $\gamma°$), and (2) estimated horizontal distance (= d_1) from the observer to the bird flock when the telescope tracking started — this normally occurred when the flock passed relatively near the observer; (3) the time of telescope tracking until the flock vanished from sight, and (4) vanishing bearing (= $\alpha°$). The flight distance covered by the birds during the time of tracking (= d_2) was estimated by assuming that birds in straight line flight (disregarding time spent in circling flight) travel with a speed of 1 km per min, which is a good approximation of the mean speed of waders as well as Brant Geese (see below).

The angle for parallax compensation (= $\beta°$) could be calculated from

$$\beta = \arcsin [d_1 \sin(\alpha-\gamma) \ d_2^{-1}]$$

The flight direction of the flock is then determined as $(\alpha + \beta)$. The angle β will be positive or negative depending

on whether the flock passed to the left or right respectively of the observer facing the vanishing bearing.

To avoid large errors in estimated flight directions we have included in our analysis only cases with an angle of parallax compensation $|\beta|$ less than $30°$ and with effective tracking time at least 3 full minutes. Flocks passing right overhead ($\beta = 0°$) have been included in orientation data if effective tracking time is at least 2 min. Median tracking time was 5 min 40 s (with maximum 17 min 15 s) for wader flocks and 9 min (max. 27 min) for flocks of Brant Geese.

As a complement to the telescope tracking data, in 1988 we used an optical range finder (WILD, 80 cm, 11.25×) with azimuth and elevation scales to determine positions of departing wader flocks at 0.3-6.0 km range. This allowed us to calculate flight and climbing speed, as well as altitude and direction, during time intervals between 1 and 6 min (mean time interval 3 min 37 s $\pm$ s.d. 75 s; n = 26 intervals) for 17 different flocks of departing waders. Directions during straight-line flight, as calculated from the range finder data, were in close agreement with flight directions estimated by telescope tracking, and we have consistently used estimates derived by the latter method in our set of orientation data.

Several flocks migrated along the coastline at Malarrif. Flight directions of such flocks clearly influenced by local topographical features have been excluded from analysis.

Unless otherwise stated, all directions refer to geographic compass directions (magnetic declination in the study area was $-24°$), and times are local Icelandic time (=GMT).

RESULTS

Number of Migrants

Altogether 303 flocks comprising 31 179 waders (Knots and Turnstones) and 77 flocks with 3178 Brant Geese were recorded departing from Iceland (Table 1). Knots were much more numerous than Turnstones; of the 16 443 identified waders, 15 086 (91.7%) were Knots and 1357 (8.3%) Turnstones. We expect a similar high proportion of Knots to occur in the wader (Knot and/or Turnstone) flocks where we could not distinguish with certainty between the two species (designated as "waders," cf. Table 1), and we have therefore frequently combined this "wader" category with that of identified Knots after ensuring that there were no significant differences in flock sizes, timing or orientation between the two categories.

Our observations were mainly designed for purposes other than counting departing migrants at each site. Still, totals of migrating waders and geese recorded during the main departure period 25-31 May indicated differences in magnitude and composition of migration among the three observation sites.

The largest number of Brant Geese, slightly more than 2000, was recorded at Malarrif, while wader migration at this site was relatively sparse, only about 1200 Knots and Turnstones being observed during the departure period in 1986. In comparison, wader migration was more prominent at Latrabjarg, where, during the same season, close to 7000 waders were recorded, often passing far offshore at high altitudes over the open sea of Breidafjördur. In contrast, fewer Brant Geese (just over 1000 individuals) were observed migrating past Latrabjarg compared with Malarrif during spring 1986. At Vatnsfjördur, intensive Knot and Turnstone migration completely dominated the scene. Total numbers of migrating waders in the 1987 and 1988 seasons were close to 16 000 and 7000 respectively. All migrants climbed and departed towards W/NW across the mountains, which means that there exists no overlap between waders at this site and those passing the tip of Latrabjarg farther to the west (cf. Fig. 1). No Brant Geese were observed at Vatnsfjördur, indicating that for this species there are no significant staging sites along the shores and islets of N and NE Breidafjördur. This is in marked contrast to the situation among the Knots, for which the latter region is of major importance as a staging area, quite comparable or even superior to favourable Knot haunts in other parts of W Iceland.

Departure Behaviour

The Vatnsfjördur area was used as a staging site by approximately 5000 Knots and 500 Turnstones during the end of

TABLE 1. Numbers and flock sizes of departing Knots, Turnstones and Brant Geese recorded 25 May–1 June at three observation sites in W Iceland (regular observations were carried out at Malarrif and Latrabjarg in 1986 and at Vatnsfjördur in 1987 and 1988)

Species	Locality	No. of birds	No. of flocks	Flock size		
				Mean	Median	Max
Knot	Malarrif	1 032	11	94	75	250
	Latrabjarg	2 898	16	181	115	600
	Vatnsfjördur[a]	10 581	120	88	65	400
Turnstone	Malarrif	116	9	13	11	25
	Latrabjarg	60	1	—	—	—
	Vatnsfjördur	767	11	70	58	140
Mixed flocks[b]	Vatnsfjördur	989	10	99	58	325
Waders[c]	Malarrif	40	1	—	—	—
	Latrabjarg[d]	3 945	21	188	150	600
	Vatnsfjördur	10 751	103	105	70	600
Brant Goose	Malarrif	2 053	52	40	33	150
	Latrabjarg[e]	1 125	25	45	28	130

[a] Including six flocks observed on 1 June 1986.
[b] 575 Knots and 414 Turnstones were recorded in mixed flocks of these two species.
[c] This category refers to flocks of Knot/Turnstone, where we could not distinguish with certainty between the two species.
[d] Including one flock observed on 31 May 1988.
[e] Including two flocks observed on 31 May 1988.

May in all three years 1986-88 (Fig. 2). Knots in a departing flock call vigorously as they take off and climb, typically in circling flight. The air is filled with loud chattering as the birds incessantly utter excited "veit-veit" calls, interspersed with occasional soft, curlew-like whistling calls. These whistling calls are typically given during song-flight display at the breeding territories (Nettleship, 1974). Flocks arriving at Vatnsfjördur were heard at long ranges, sometimes 2-3 km. On repeated occasions we saw two or more flocks of Knots uniting into a single large flock during the circling flight, presumably as a result of mutual responses to callings from flocks in the vicinity.

FIG. 2. A flock of Knots departing from the seashore of West Iceland. Photo: J. Karlsson.

Turnstones behaved much as the Knots when departing and climbing from Vatnsfjördur. Flight calls from Turnstone flocks differ characteristically from those of Knots, but sound level and range are about the same for the two species.

At Vatnsfjördur the Knots and Turnstones are confronted with a passage 12-50 km across land, rising 500-700 m asl, before the birds reach the fjords of the NW Icelandic coast or the open Denmark Strait. Before this passage the waders climb steeply. Knots not only used flapping flight during this climbing phase, but to a surprisingly high degree adopted gliding or soaring to obtain lift from thermals or slope and lee waves. Sometimes the Knots gained height by almost pure thermal soaring, gliding in tight circles with their wings fully spread and completely without wing beats.

The Knots used circling flight up to between 400 and 940 m asl (mean altitude 600 m ± s.d. 150 m, n = 14 flocks), at which altitude they changed to straight-line flight, still climbing, in their migratory direction. Not only flocks departing locally from the Vatnsfjördur shores adopted circling flight up to these altitudes, but flocks arriving from the east at low or moderate heights, often 150-500 m, also stopped to circle for several minutes to increase their height. The rate of climb during circling flight varied between 0.45 and 1.75 m·s⁻¹, with a mean at 1.12 ± 0.43 m·s⁻¹ (n = 15). Generally the birds moved slowly in their intended direction while flying in rather wide circles, sometimes flying off some distance before resuming circling. The resulting ground speed during circling flight varied between 1.9 and 12.0 m·s⁻¹, with a mean speed at 6.6 ± 2.7 m·s⁻¹ (n = 15).

Knot flocks continued to climb when departing over land in straight-line flight. However, rate of climb was slower, between 0.47 and 0.96 m·s⁻¹ (mean 0.72 ± 0.20 m·s⁻¹, n = 7),

while ground speed was much faster, 10.1–19.7 m·s⁻¹ (mean 15.8 ± 3.4 m·s⁻¹, n = 7), than during the preceding circling flight. As expected, flocks in level flight showed an even faster mean ground speed, viz., 17.7 ± 2.7 m·s⁻¹ (range 15.5–21.4 m·s⁻¹, n = 4 flocks).

Heights at the point of vanishing from sight at Vatnsfjördur were estimated for 61 wader flocks on the basis of readings of the telescope elevation angle and calculated distances. Most flocks that circled to gain height over Vatnsfjördur finally disappeared in the migratory direction at heights between 400 and 1200 m asl (46 out of 61 flocks). For 8 of the 61 flocks, vanishing altitudes were estimated between 1200 and 2000 m asl, the three highest records being 1600, 1750 and 1990 m. Although the vast majority of these estimates refer to flocks of Knots, 4 flocks of Turnstones are included in the data, with vanishing altitudes between 550 and 1750 m asl.

Observations at Latrabjarg and Malarrif confirm the waders' preference for high cruising altitudes, but also demonstrate that they may descend low over the sea, depending on wind conditions. Out of 32 wader flocks, 16 were observed departing over the open sea off Latrabjarg at estimated altitudes of 500-1000 m asl, or even higher. Eight flocks passed at intermediate heights, between 100 and 400 m asl, while the remaining 8 flocks travelled at lower altitudes, 5 of them descending to fly immediately above the sea surface as they encountered unfavourable crosswinds off the westernmost tip of Iceland.

At Malarrif, 14 out of 19 flocks of Knots and Turnstones climbed as they took off from nearby shores or arrived low along the coastline. These flocks reached several hundreds of metres in altitude and continued to climb as long as they were seen. Only 5 flocks were observed passing in low altitude coastal flights.

There is a distinct difference in flight altitudes between the waders and Brant Geese, the latter generally travelling at lower heights and being more prone to following coastlines. At Latrabjarg, 12 out of 21 flocks of Brant Geese were seen departing over the open sea at low altitude, 8 flocks maintained heights between 100 and 400 m asl, while only a single flock was observed flying at greater heights. At Malarrif, 46 out of 52 Brant Geese flocks passed at altitudes below 100 m asl, some of them climbing as they left the coastline behind them. Of the 52 flocks, 35 were flying closely along the shoreline past the observation site.

Flock Sizes

The waders, as well as the Brant Geese, travel in flight formations, mostly echelon, V- or U-formation. The latter formation, where birds fly on curved, bow-shaped fronts (cf. Hummel, 1973), is more common than strict V-formation. Large flocks most often showed branched compound formations, with the configuration changing continuously in a winding and undulating way.

Mean and maximum flock sizes and the distribution of flocks and individuals in different flock size classes are presented in Tables 1 and 2 respectively. For the Knot, the mean flock size at both Malarrif and Vatnsfjördur was close to 100 birds, while it was about twice as large at Latrabjarg (categories Knot and waders in Table 1). As might be expected from their sparser occurrence, Turnstones did not migrate in such large flocks as the Knots. Only 4 of 21 Turnstone flocks exceeded 100 birds in size, the largest one numbering 140 birds, but these 4 flocks together held just above half

TABLE 2. Relative distribution of number of flocks and individuals of migrating Knots, Turnstones and Brant Geese in flock size classes

	Flock size							
	1-9	10-24	25-49	50-99	100-199	200-399	400-799	N[a]
Flocks (%)								
Knot (incl. waders)	2.2	11.4	15.8	33.1	20.2	13.6	3.7	272
Turnstone	9.5	42.9	14.3	14.3	19.1	0	0	21
Brant Goose	16.9	24.7	31.2	15.6	11.7	0	0	77
Individuals (%)								
Knot (incl. waders)	0.1	1.8	5.2	20.7	24.5	31.1	16.8	29247
Turnstone	1.4	15.1	12.2	19.9	51.4	0	0	943
Brant Goose	2.7	10.4	27.9	24.4	34.8	0	0	3178

[a] Total number of flocks and individuals.

of the total number of Turnstones recorded in pure flocks. Although the Knots and Turnstones that migrated together in mixed flocks usually formed part of a common flight formation, individuals of the same species normally kept together in a subgroup within the common flock.

There is a good agreement between the observation records from Malarrif and Latrabjarg that Brant Geese depart from Iceland in flocks with a mean size of about 40 birds and with maximum sizes of 130 to 150 birds.

Seasonal and Daily Timing

The main exodus from Iceland of Knots, Turnstones and Brant Geese occurred during the period 25-31 May in all three spring seasons 1986-88. Although we did not undertake systematic observations of migration before 25 May, we carried out extensive field work during the previous weeks and would certainly have detected any significant departures. In 1987 we recorded two flocks of Turnstones climbing to great heights and leaving on 23 May.

Although Knots, Turnstones and Brant Geese were recorded throughout the study period 25-31 May, our observations indicate small differences in average seasonal timing among the species. Turnstones appeared to depart slightly before Knots, which were simultaneous with or possibly slightly earlier than the Brant Geese. Combining data from all three years, the median departure date was 26 May for Turnstones and 28 May for Knots and Brant Geese. The proportions of departing migrants that we recorded during the first two days, 25 and 26 May, of the study period were 52% for Turnstone, but only 9% and 1% for Knot and Brant Goose respectively. In comparison, during the final days of our observation period, 30 May-1 June, only 7% of the Turnstones were recorded, while the corresponding proportions for Knots and Brant Geese were 14% and 43% respectively. By 1 June the coastal staging sites were almost empty of Knots and Turnstones, only very small numbers remaining where just a few days earlier a multitude of noisy birds filled the scene.

As seen from Figure 3, departures generally took place in the afternoon and evening, although in 1986 there was a secondary peak, most prominent for the Brant Goose, in the morning or about noon. The average daily timing of wader departures differed significantly between years, taking place relatively late in the day in 1986 (median time 20.20 h) but considerably earlier in 1987 (median 18.20 h) and earlier still in 1988 (median 17.10 h). These differences appeared to be associated with the temporal displacement of the tidal cycle between years, the waders preferring to depart during rising or high tide. This is clearly indicated

in Figure 3, where the daily tidal variation is shown for the peak day of wader migration in each year. The tidal cycle is displaced on average about 50 min later each successive day, which means that not only the main peak but also the secondary peak of wader migration in 1986, recorded only during the last days, 30 May to 1 June, in that season, occurred during rising tide.

There is a distinct tendency for the waders to depart earlier in relation to high tide with the progress of the season. This effect was consistent in all three years and is shown in Figure 4, with data from all years combined. Average departure time approximately coincided with high tide on 26 May, gradually changing to 2-4 h before high tide on 29 and 30 May. The average solar departure time changed relatively little between consecutive days *within* a season (Fig. 4; although there were clear differences in daily timing *between* seasons, as earlier pointed out; cf. Fig. 3).

Flight Directions

Our measurements of departure directions showed a high degree of conformity between different observation sites and species. The mean orientation falls very close to 300° for the Knot, Turnstone and Brant Goose, with directional scatter corresponding to an angular deviation of 21-26° (Table 3). The distribution of flocks and proportions of individuals departing in different directions are presented in Figure 5.

The great majority of the birds departed in the sector 280-330°, the proportion of individuals being 74, 51 and 77% for the Knot, Turnstone and Brant Goose respectively. Within this sector, there is a concentration of flocks and individuals in the narrow range 290-310°, where 37, 36 and 59% of the Knots, Turnstones and Brant Geese respectively were seen to depart. Departures in WNW-NW directions imply that the birds were following routes traversing the Greenland inland ice towards breeding destinations in Canada and NW Greenland (cf. Discussion section below). In contrast, flight directions in the sector 340-010° point towards migration to quite a different part of the breeding range for the three species concerned, i.e., NE/E Greenland (e.g., Salomonsen, 1950, 1967; Meltofte, 1985). There is an indication of a secondary peak of departure directions in this sector for the Turnstone, encompassing 19% of the individuals. In comparison, only 5 and 7% of the Knots and Brant Geese respectively departed in this sector.

In most instances, the weather was favourable for orientation, with good visibility and the sun clearly visible. However, there were a few exceptional occasions. In the late afternoon of 28 May 1988, cloudiness was considerable (stratocumulus, with base and top about 900 and 1200 m
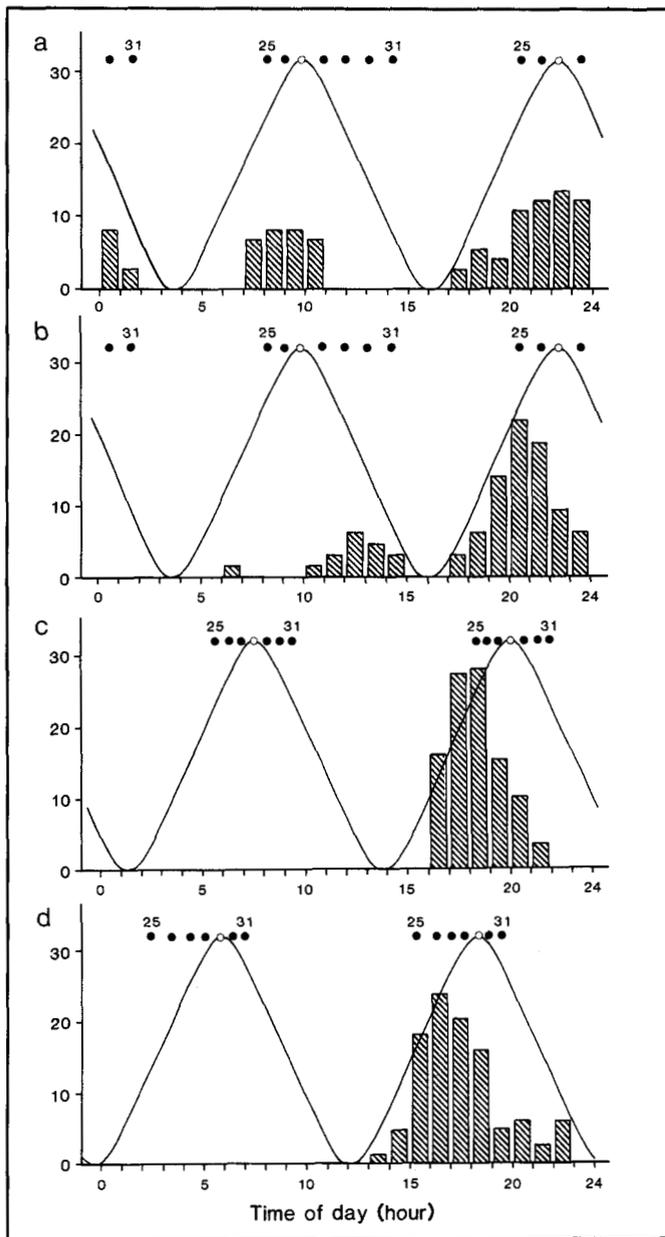
FIG. 3. Daily timing of departure from Iceland 25 May–1 June of Brant Geese in 1986 (a) and of Knots and Turnstones combined in 1986 (b), 1987 (c) and 1988 (d). Hatched bars show the percent distribution of departing flocks during the different hours of the day (local Icelandic time = GMT). The histograms (from top to bottom) are based on 75, 64, 149 and 90 flocks respectively. The local tidal cycle on the day of peak migration is schematically indicated by curves. The tidal cycle is displaced later each successive day, and high tide on different dates 25-31 May is indicated by dots. (Tidal information from Sjavarföll vid Island 1986, 1987, 1988, Sjomaelingar Islands, Reykjavik).

respectively), although visibility was very good. There were only a few distant gaps in the cloud layer, mainly along the western horizon, and it was quite impossible for a human eye to determine the position of the sun. In spite of this, migration of well-oriented wader flocks was intensive, and 23% of the seasonal total of departing waders was recorded on this day. We repeatedly suspected that migrants climbed through the cloud layer, as flocks at high altitude suddenly vanished from sight.

The most remarkable instance of departures in poor weather occurred between 12.30 and 14.30 h on 1 June 1986, when six flocks totalling 448 Knots climbed into low clouds at Vatnsfjördur. Complete overcast prevailed, comprising 8/8 stratus with base not much higher than 50 m asl. Furthermore, it was raining constantly, with varying intensity. The Knots were departing in the warm sector of a cyclone, close to the low pressure centre. Meteorological evaluation (Bertil Larsson, pers. comm. 1986) suggested that the overall weather situation probably was as follows: rain was falling from moderately high clouds (base ≥ 2000 m asl, altostratus, altocumulus castellanus) in a conveyer belt in front of the cold front. Below was a layer of stratus extending from 50 m up to 300-600 m asl.

The Knots arrived at Vatnsfjördur at low altitude along the coast, where they behaved in the typical way. They called vigorously, started to circle and soon disappeared straight up into the clouds over the western and northwestern slopes of this fjord. Small and scattered parties reappeared, dropping out of the clouds a few minutes after each flock had disappeared; these birds subsequently landed along the shore or flew east in return migration and comprised 123 (27%) of the 448 individuals recorded. The majority of the Knots apparently continued up through the clouds and across the mountains. Never before have we witnessed birds climbing so directly and purposefully into compact clouds, during constant rain, than did these Knots at Vatnsfjördur. These observations show that the waders are capable of assuming a departure orientation that is at least broadly correct in spite of complete overcast and poor visibility.

DISCUSSION

Flight Altitude and Speed

Upon departure from Iceland, Knots and Turnstones climb steeply to high altitudes, setting off in their migratory direction straight across land or sea, largely unaffected by coastal topography. One important advantage of climbing to great heights may be that the waders can sample winds as they go in order to choose altitudes where winds are most favourable, as suggested for migrating terns by Alerstam (1985).

Waders are renowned for migrating at high altitudes (cf. Richardson, 1979). Flocks of Siberian Knots registered by radar during spring migration at Helsinki in S Finland most often passed at altitudes between 500 and 2000 m, the highest record being close to 3000 m (Dick et al., 1987). Although high altitude migration is probably preferred by shorebirds, they certainly show a readiness to descend and migrate at low altitudes and to follow coastal leading lines, most often when winds are unfavourable.

A high climbing capacity allows the waders to reach high altitudes quickly. The rate of climb for departing Knots in Iceland varied between 0.45 and 1.75 m·s^{-1} (overall mean climb rate = 1.0 m·s^{-1} ± s.d. 0.4 m·s^{-1}, n = 22). These climb rates almost match those of Arctic Terns Sterna paradisaea (with mean climb rate = 1.2 ± 0.4 m·s^{-1}), which were tracked by radar when departing across land in S Sweden (Alerstam, 1985).

Waders depart from Iceland with very heavy fat reserves, an added weight that must significantly impair their climbing performance (Pennycuick, 1975, 1978; Videler et al., 1988).
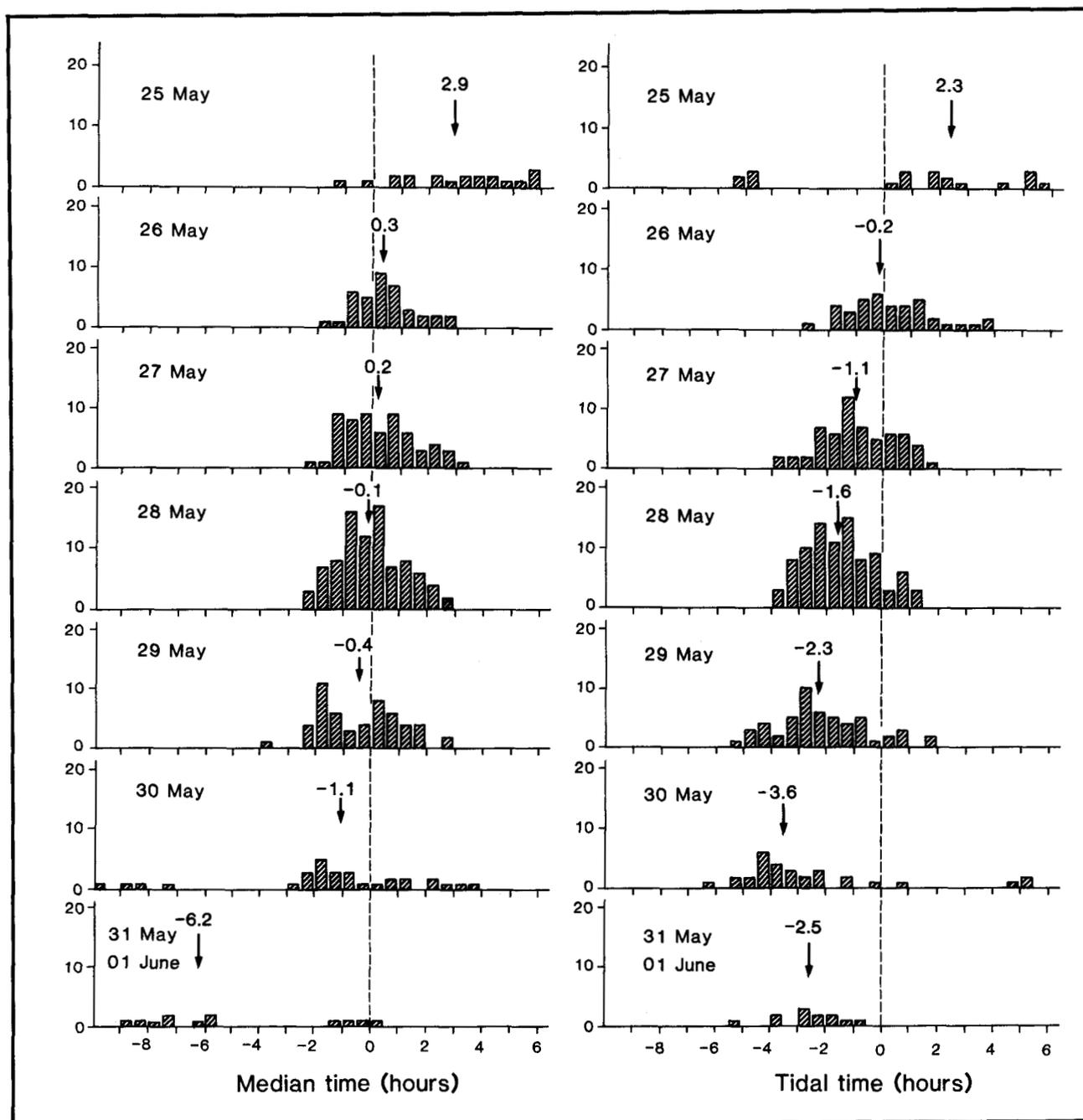
FIG. 4. Within-season variation in daily timing of wader departure 25 May–1 June. Hatched bars show the number of departing flocks of Knot and Turnstone on different dates for the three years 1986-88 combined. Diagrams to the left show the distribution in relation to the seasonal median daily departure time. To the right is the distribution in relation to the time of high tide. Arrows indicate median time displacements from the seasonal median time and time of high tide.

That they can climb even faster than recorded in Iceland, when migrating with smaller fat reserves, is supported by a few tracking radar measurements from S Sweden in late July (unpubl. data; equipment and recording technique according to Alerstam, 1985). One mixed flock with six Knots and six Dunlins *Calidris alpina* climbed from 190 to 970 m asl during 630 s when departing inland in straight-line flight, giving a mean climb rate of 1.24 m·s⁻¹. The flock was still climbing when lost by the radar. Two Turnstones departing inland climbed steadily from 290 to 930 m asl in 430 s, i.e., by 1.48 m·s⁻¹, in straight-line flight, again continuing to climb until lost by the radar.

Mean air speed of the above-mentioned two flocks was 15.4 and 14.8 m·s⁻¹ respectively. These flight speeds are in reasonable agreement with our speed measurements from Iceland. Three flocks of Knots tracked by radar in level flight across S Sweden showed mean air speeds 16.4-20.3 m·s⁻¹, which is also similar to estimates of level flight speed from Iceland. Flight speed estimates from Iceland refer to ground speed, since lack of information about winds at different altitudes made it impossible to correct for the effect of wind. Noer (1979) reported a mean air speed at 15.8 m·s⁻¹ for Knots migrating at low altitude along the coast in calm weather. Air speed increased with opposed winds (and

TABLE 3. Mean orientation and directional scatter of flocks of Knot, Turnstone and Brant Geese departing from W Iceland in spring 1986-88 (mean vector and angular deviation have been calculated according to Batschelet, 1981)

Species	Locality	Mean vector (deg.)	Mean vector length (r)	Angular deviation (deg.)	Number of flocks
Knots (incl. waders)	Malarrif	289	0.98	11	7
	Latrabjarg	310	0.95	19	18
	Vatnsfjördur	297	0.89	27	87
	All	298	0.90	26	112
Turnstone	Malarrif	300	0.99	7	6
	Vatnsfjördur	294	0.86	30	7
	All	297	0.92	23	13
Mixed flocks[a]	Vatnsfjördur	304	0.91	24	7
Brant Goose	Malarrif	290	0.98	10	17
	Latrabjarg	313	0.92	23	16
	All	301	0.93	21	33

[a] Mixed flocks of Knot and Turnstone.

with increasing flock size) to about 19 m·s^{-1} in moderate headwinds.

Our observations from Iceland showed that the Brant Geese generally migrated at lower altitudes, and were more prone towards following coastlines, than the waders. Johnson et al. (1975) recorded intensive eastbound spring migration of Brant Geese Branta bernicla nigricans at the southern coast of the Beaufort Sea in NW Canada, with 74% of all birds flying only a few metres above the ground or ice. Only a few flocks were observed at altitudes as high as 100 m or above. Large numbers of Brant Geese Branta b. bernicla, migrating between winter quarters at the North Sea and breeding sites in Siberia, regularly fly at low altitude along coastlines in the Baltic Sea during spring as well as autumn migration (pers. obs.). In contrast, the majority of arctic waders pass unnoticed at high altitudes, except in years when they encounter unfavourable weather in this region (Roos, 1975).

Tracking radar registrations of Brant Goose flocks departing across land during autumn migration in S Sweden show that they most often climb to heights in the range 200-500 m asl before resuming level flight (Alerstam, unpubl. data).

Why do the geese often migrate at lower altitudes than the waders? One relevant factor may be the climbing capacity. For flight mechanical reasons, climbing capacity is expected to relate negatively to body size among birds (Andersson and Norberg, 1981). Climb rates as registered by tracking radar for migrating Brant Geese in S Sweden, with a mean at 0.56 m·s^{-1} (s.d. = 0.19, sample of 29 flocks, Alerstam, unpubl. data), are distinctly lower than found among arctic waders. Because of their heavy fat loads, Brant Geese departing from Iceland would be expected to achieve even slower climb rates than the above mean. Still, it is necessary that the geese have the capacity to climb to several thousands of metres of altitude, since after departing from Iceland, they fly across the Greenland inland ice, which rises to heights about 3000 m asl.

Formation of Flocks

Comparison of sizes of wader flocks departing from Iceland (Tables 1 and 2) with flock sizes reported for birds arriving in NW Greenland and Ellesmere Island indicates that the large flocks break up into smaller units when the birds approach their destination. Ferdinand (unpubl. report cited in Meltofte, 1985) observed Knots and Turnstones

arriving from the sea at Kap Atholl in NW Greenland (31 May and 2 June 1964) in flocks of 2-50 birds. The average size for seven flocks of Knot was 16 individuals, for nine flocks of Turnstone 12 individuals and for four mixed flocks 20 individuals. Nettleship (1974) reported seven flocks of Knot ranging in size from 6 to 60 birds, with a mean of 27 individuals per flock, arriving at Lake Hazen, Ellesmere Island (5 June 1966). Similarly, flock sizes were relatively small among Knots (mean = 37 individuals; n = 30) and Turnstones (mean = 11 individuals; n= 27) arriving at the southwestern coast of Iceland in late April/early May 1987-88 (Gudmundsson, unpubl. data).

Flocks of Brant Geese may remain intact throughout the long flights to the breeding sites to a higher degree than the wader flocks. Mean flock size was 55 individuals for 24 Brant Goose flocks observed when arriving in SW Iceland in early May 1987-88 (Gudmundsson, unpubl. data). Johnson et al. (1975) noted that during spring migration Branta bernicla nigricans passed the coast of the Beaufort Sea in rather large flocks. Fifty-four percent of the flocks consisted of 25 birds or more, and 54% of all individuals were in flocks of more than 105 birds. The corresponding proportions are similar for departing Brant Geese in Iceland (Table 2).

It is well known that Knots and Brant Geese sometimes travel in very large flocks, especially when migrating from spring staging areas where huge numbers of birds are concentrated, like the North Frisian Wadden Sea (Prokosch, 1984, 1988). Meltofte and Lyngs (1981) observed Knots departing from this area towards Iceland and/or N Norway (cf. Davidson et al., 1986; Prokosch, 1988) between 8 and 14 May 1973. Mean flock sizes varied between 217 and 413 individuals on different days. The two largest flocks consisted of about 2000 and 2300 Knots. As well, large flocks of Siberian Knots have been observed departing in the first half of June from the Wadden Sea across Scandinavia and S Finland. At one observation site in the Gulf of Finland between 3 and 17 June 1979 the overall mean flock size was 800 individuals (Dick et al., 1987).

Such large flocks are probably formed only at staging sites with the highest concentrations of migrants. Whitfield and Magnusson (1987) studied spring departures of Knots and Turnstones from a staging site of less importance, in NE Iceland, used by up to 8000 Knots and 10 000 Turnstones. Mean sizes of departing flocks were 25 individuals for Knot (n = 12), 24 individuals for Turnstone (n = 23) and 46 individuals for mixed flocks (n = 30).
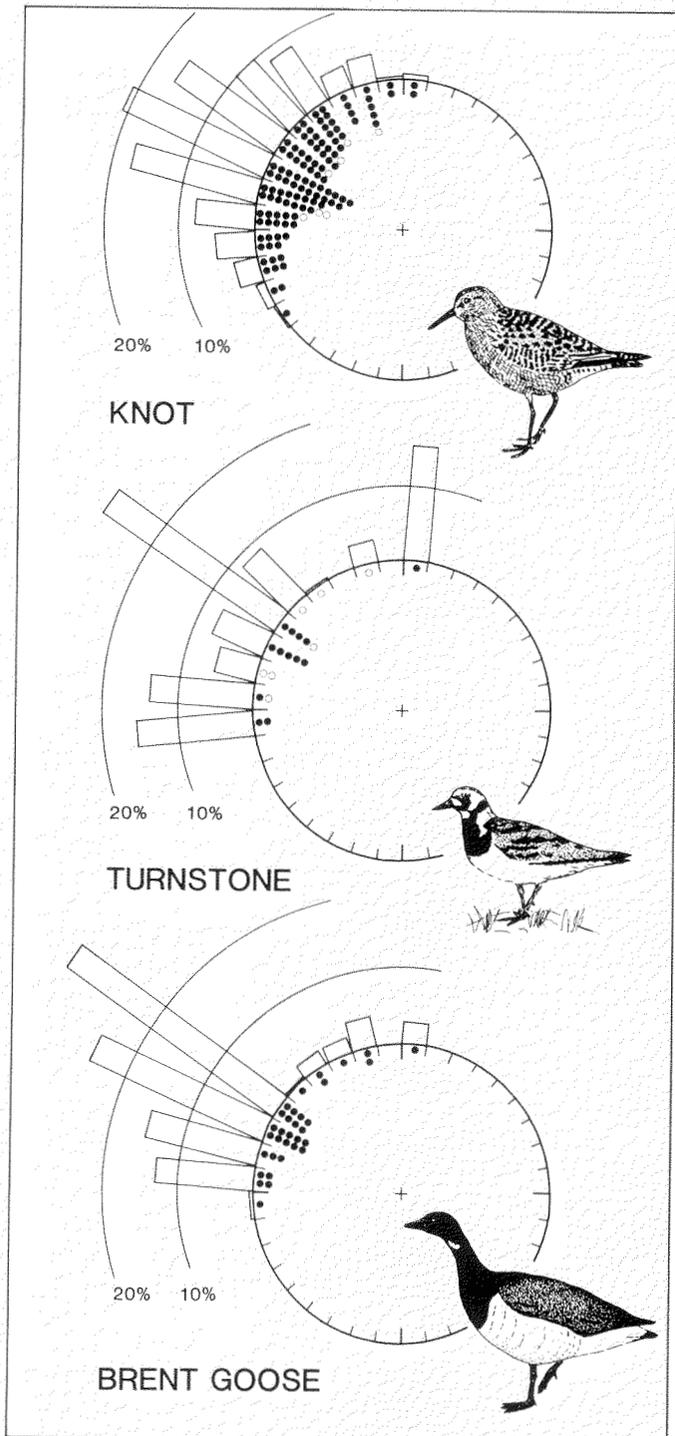
FIG. 5. Orientation of Knots, Turnstones and Brant Geese departing in spring from W Iceland. Data are grouped into 10° sectors. Dots indicate departing flocks, while bars show the percent distribution of individuals in different sectors. Open dots refer to mixed flocks of Knots and Turnstones (cf. Table 3).

What are the most important factors promoting the formation of flocks, as observed among the departing waders and Brant Geese?

(1) Formation flight improves aerodynamic efficiency and leads to a considerable reduction of flight power. Lissaman and Shollenberger (1970) calculated that cost of transport would be reduced by 30-40% for members of flocks with 9-25 individuals in formation flight, in comparison with cost of flight transport for a lone bird. Hummel (1973, 1983) calculated corresponding reductions in total flight power at 20-25%. On the basis of photography of 56 Brant Geese in characteristic formation positions, Hummel (1973) calculated an average power reduction of 18% for the flock members. The above estimates imply that for a given amount of fuel reserves carried by the birds, a flock may have a range increase of 20-70% in comparison with a single bird. The bow-shaped, modified V-formations promote an equal distribution of energy savings among the flock members (Hummel, 1983). Even if power reduction associated with formation flight increases with flock size, the marginal increase in benefit with increasing flock size above about 30 birds is small (Lissaman and Shollenberger, 1970; Hummel, 1983).

(2) Social stimulation and the urge to gather in large flocks upon departure may serve to reduce the seasonal time scatter in migratory activity and to synchronize the internal annual migratory rhythm among the birds. Arctic migrants depart on their long, final, spring flights to the breeding sites within a very narrow seasonal time window (departures from Iceland are mainly 25-31 May), which is remarkably constant from year to year (Salomonsen, 1967; Meltofte, 1985; Alerstam et al., 1986). From their distant starting positions the birds have little possibility to adjust the timing of their departure to yearly variations in the progress of spring at the destinations in the polar climatic zone. Social stimulation will act to concentrate departure at the mean endogenous time for the population.

(3) Accuracy of orientation towards the intended mean direction of the population may be higher for birds in flocks in comparison with single individuals and may increase with increasing flock size (Bergman and Donner, 1964; Hamilton, 1967; Wallraff, 1978; Tamm, 1980). For the Knot there is indeed a tendency for the largest flocks to show the smallest scatter in orientation. The angular deviation for small flocks, up to 30 individuals, was 30° (n = 25 flocks). For medium-sized flocks, with 30-150 individuals, it was 26° (n = 61), and the largest flocks, with 150-600 individuals, showed an angular deviation of 19° (n = 26 flocks). However, the difference in angular deviation was not statistically significant between the small- and medium-sized flocks (F = 1.37, p > 0.05, Watson-Williams test for the concentration parameter; Batschelet, 1981), and only marginally so between medium-sized and large flocks (F = 1.78, p = 0.06) and between small and large flocks (F = 2.43, p < 0.05). The Turnstone and Brant Goose showed no consistent or significant differences in angular variance between flock size categories.

Another possible advantage associated with migration in flocks is that older, experienced birds among the flock members can control the orientation with reference to familiar landmarks.

Daily Timing of Departure

The Knots and Turnstones departed from Iceland during (a) the afternoon and evening and (b) rising or high tide (Figs. 3 and 4). The mean daily time of departure varied considerably among years, depending on the tidal cycle. In 1987 and 1988, when high tide occurred early in the afternoon or evening, most waders departed already between 9 and 4 h before sunset (local time of sunset about 23.30 h). During the study period the 24 h day in NW Iceland is divided into approximately 20 h of daylight and 4 h of civil twilight.

In 1986, when high tide occurred as late as midnight, most waders departed during the 3 or 4 h preceding sunset. In this year there was also a secondary peak already around noon (Fig. 3), appearing mainly during the late part of the departure period, i.e., 30 May–1 June. The situation during this period probably marks the transition when the waders shift their departure from one high tide cycle to another, as the late-evening high tide becomes progressively displaced to late after sunset/midnight.

There are several reports that *Calidris* waders and Turnstones usually depart on migration a few hours before sunset. In a few cases it has been noted that departures also tend to be associated with incoming or high tide (Ferns, 1979, 1980; Dick *et al.*, 1987; Lank, 1989). During autumn migration along the shores of the Baltic Sea, where there is practically no tidal variation, Knots and Turnstones show a peak of departures from about 3 h before sunset to sunset (Edelstam, 1972). At the Wadden Sea, major departures of Nearctic Knots have been observed during the 2 h before sunset on 8-14 May (Meltofte and Lyngs, 1981) and of Siberian Knots between 3 and 1 h before sunset on 2-10 June (Dick *et al.*, 1987).

In contrast to the waders, the Brant Geese showed a distinctly bimodal daily pattern of departure activity, with flocks leaving Iceland both in the morning and evening. Siberian Brant Geese are commonly observed passing southern Scandinavia during spring migration in the early part of the day, demonstrating that they, in contrast to the waders, regularly depart also in an early morning peak (Prokosch, 1984).

Knots, Turnstones and Brant Geese change between foraging and roosting activities in response to the tidal cycle at their staging sites. The tidal amplitude at Vatnsfjördur is between 1.8 and 3.9 m (neap and spring tide respectively). Hence, it seems entirely reasonable that the birds are most prone to depart after having foraged during a low tide period and when starting to assemble at the roosting sites. Why, in addition to this tidal influence, the waders prefer to depart during afternoon or evening hours, while Brant Geese are prepared to leave also in the morning, is more difficult to understand. Possibly night-time foraging is less efficient among the waders as compared to the Brant Geese. This would make it extra important for the waders always to utilize the day-time low tide period for foraging before departure (cf. Lank, 1989). Our observations from Iceland show that departures of Knots and Turnstones can be less tied to the hours immediately preceding sunset than has hereto been reported.

Destination Areas

It has earlier been maintained that the large numbers of Knots, Turnstones and Brant Geese resting in Iceland in spring are destined for two major parts of the breeding range, i.e., NE/N Greenland (in the sector 340-010° from W Iceland) and NE Canada/NW Greenland (280-330° from Iceland) respectively (Salomonsen, 1950, 1967; Morrison, 1975, 1977; Wilson, 1981; Meltofte, 1985). However, the relative importance of these two main migratory pathways from Iceland has remained unknown. Our data (Table 3, Fig. 5) provide a clear-cut and perhaps surprising answer to this question: The vast majority of flocks and individuals of all three species travel towards breeding regions in NE Canada/NW Greenland. Only a minority are oriented

towards the NE/N Greenland part of the breeding range. The small proportions of birds orienting in the sector 340-010° may not necessarily represent migrants destined for NE/N Greenland, since it is also possible that the northerly directions are only temporary course deviations, adding to the scatter of a unimodal orientation centred around 300°.

The majority of Knots and Turnstones at a staging site in NE Iceland also departed towards WNW (Whitfield and Magnusson, 1987), which indicates that they probably joined the birds from W/NW Iceland on the flight route to Canada and NW Greenland. There was, however, also a secondary peak of waders orientating from NE Iceland towards the NE Greenland breeding sector, constituting about one-third of the Turnstones and one-tenth of the Knots respectively (Whitfield and Magnusson, 1987).

Why is the migration link between Iceland and the NE/N Greenland breeding range of such limited importance, in spite of the fact that the associated flight distance is much shorter than the distance across the Greenland inland ice to Canada and NW Greenland? One possibility is that breeding populations in the former region are very small in comparison with the large numbers of birds breeding in N Canada and NW Greenland. This is probably true for the Brant Goose, which has become greatly reduced in numbers in NE/N Greenland during this century (Meltofte *et al.*, 1981; Håkansson *et al.*, 1981). Only recently was an important breeding concentration of at least 250 pairs of Brant Geese discovered at the northeasternmost point of Greenland (Hjort *et al.*, 1987). However, the Knot and Turnstone are widely distributed over at least 60 000 km^2 of suitable breeding habitat in NE/N Greenland (Meltofte, 1985).

Another possible explanation is that many birds destined for NE/N Greenland reach their goal, not via Iceland, but via alternative staging areas. This may apply to the considerable numbers of Turnstones that deposit large fat reserves before departing from the Irish Sea during the last days of May (Clapham, 1979; Prater, 1981) and to Knots departing from N Norway (Davidson *et al.*, 1986; Uttley *et al.*, 1987). Interestingly, there is a distinct turnover of staging Turnstones at the Irish Sea (Morecambe Bay) in May, with most birds that have spent the winter in the area leaving in early May (probably flying to Iceland), while new passage birds come in to leave during the end of the month (Branson *et al.*, 1978; Clapham, 1979).

One may speculate that Iceland is thus of crucial importance as a staging area for waders and geese destined for breeding sites in N Canada and NW Greenland. It may be advantageous for these birds to winter within relatively close reach of Iceland, i.e., in Britain, Ireland and surrounding regions in W Europe, from where they can arrive in Iceland sufficiently early for the necessary fat deposition. Birds wintering at more southerly latitudes would have to initiate premigratory fattening unduly early in spring to be able to arrive in time for the refuelling time schedule in Iceland. Birds breeding in less distant arctic regions, such as NE Greenland (or regions with a later spring development), which they can reach without having to refuel in Iceland, can afford to migrate to more southerly (and perhaps more favourable) winter latitudes and still be back in time at their breeding destination. This situation may apply not only to the Turnstone but also to the Sanderling *Calidris alba* (cf. Prater, 1981; Wilson, 1981).

N Norway is not much farther away than Iceland from NE/N Greenland and may constitute a favourable alternative staging area for Knots breeding in this region, especially in view of the fact that winds are often unfavourable for a flight from W Iceland to NE Greenland (Alerstam *et al.*, 1986). Knots destined for northern and northeasternmost Greenland, as well as for Svalbard, would have a shorter flight distance from N Norway than from Iceland (Alerstam *et al.*, 1986). Hjort *et al.* (1987) suggested that the Brant Geese breeding in northeasternmost Greenland were associated with the Svalbard population of this species, migrating via Norway rather than via Iceland.

Flight Routes and Orientation Cues

The difference between a rhumbline route (loxodrome) and the corresponding great circle route (orthodrome) is most pronounced at high latitudes. The rhumbline is the path of a constant geographic bearing between two points on the earth's surface intersecting all lines of longitude at the same angle. In contrast, the great circle is always the shortest path between two points on a sphere. Travelling along a great circle route requires that the geographic course is continuously changed (about calculation of rhumbline and great circle see, e.g., Imboden and Imboden, 1972).

In this section we will show that our results imply that the birds travel approximately along a rhumbline route from Iceland to the breeding grounds. This is surprising because the simplest celestial or magnetic orientation rules would be expected to take the birds on great circle routes, as will be demonstrated below. The discussion serves to throw light on the unique problems of orientation in arctic bird migration in general and on the difficulties of explaining the birds' orientation along their flight route between Iceland and N Canada in particular.

Our data about the departure orientation at Iceland (Table 3, Fig. 5), in conjunction with radar observations from the E Greenland coast (Alerstam *et al.*, 1986) and ringing information (Fig. 6), allow us to establish with reasonable accuracy the actual trajectory of the main migratory pathway between Iceland and N Canada. That the main migratory pathway runs close to the 300° rhumbline is supported by the following facts: (1) The mean departure orientation at Iceland falls close to 300° in the Knot, Turnstone and Brant Goose flocks, with a substantial proportion of the migrants orienting in the narrow sector between 290° and 310° (Table 3, Fig. 5). (2) The median direction of radar echoes from W-NW migrating bird flocks at Sermilik at the E Greenland coast (66°20′N, 38°W) was 301°, with more than two-thirds of the echoes in the sector 290-310°. Sermilik is probably passed only by the southern flank of the WNW-bound stream of of Knots, Turnstones and Brant Geese from Iceland; no radar echoes were detected from bird flocks passing to the south of Sermilik Fjord. Wind drift over Denmark Strait may have enhanced the magnitude of passage at Sermilik, especially in one of the two spring seasons studied (Alerstam *et al.*, 1986). (3) Large numbers of migrants pass the Disko and Umanak regions in W Greenland, according to ringing recoveries (Fig. 6) as well as field records (Salomonsen, 1967). (4) The major breeding destinations on the Queen Elizabeth Islands in Canada and the Thule region in Greenland fall between or closely around the 290° and 310° rhumblines from Iceland (cf. Fig. 7).
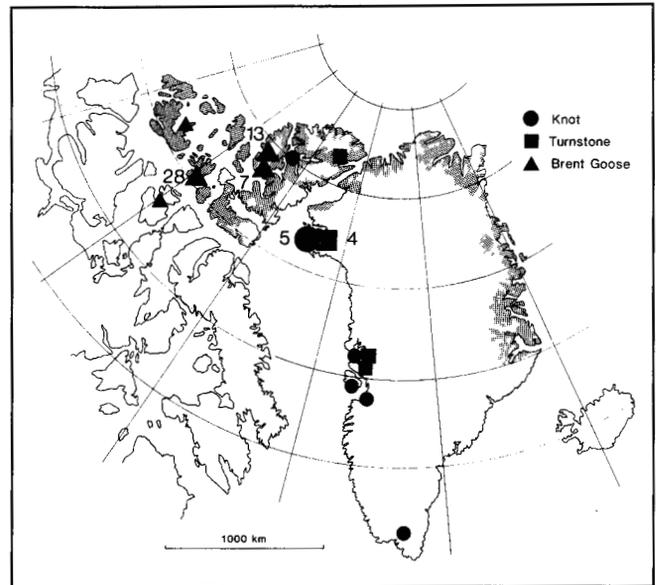
FIG. 6. Sites of ringing/colour marking/recovery in the Nearctic region of Knots, Turnstones and Brant Geese observed/recovered/ringed during migratory passage in Iceland. Sites with multiple records, as given by the figures, are indicated by enlarged symbols. Shaded areas show the main breeding range (ice-free areas) of Nearctic waders and geese wintering in Europe. Based on ringing data from Icelandic Museum of Natural History.

How does this migration route approximately following the 300° rhumbline compare with the great circle route? The distance along the 300° rhumbline from W Iceland (65°N, 24°W) to SE Ellesmere Island/NE Devon Island (77°N, 90°W) is 2665 km. In comparison, the great circle route between these two points is 2535 km (Fig. 7a). Hence, other things being equal, the migrants would save 130 km, corresponding to about 2 h of flight in calm weather, by following the great circle rather than the rhumbline route. With an air speed about 60 km·h⁻¹ the migrants need almost two full days, or 44 h, to complete the flight journey along the rhumbline.

In order to follow the great circle shown in Figure 7a, the birds should depart from Iceland with a 328° heading, continuously changing their course to approach the destination point with final heading 265°. One might suspect that the difficulties involved in great circle navigation may be an important reason why the birds prefer a longer track, close to the rhumbline, which at least superficially may seem to represent an easier option from an orientation point of view. However, closer consideration leads us to quite the opposite conclusion: There are simple orientation rules that allow the birds to migrate close to the great circle route, but, in contrast, it is difficult to imagine a simple means of orientation along the rhumbline. There are at least two obvious possibilities of great circle orientation:

(1) At latitudes close to the north or south poles it holds as a good approximation that course changes along great circles are almost equal to the associated longitudinal displacements. Hence, the course change along a great circle is approximately one degree for each degree of longitude traversed. The course change is to the left for movements in westerly directions and to the right for easterly directions of movement. This can be easily proved, considering the fact that around the poles spherical geometry can be approximated by planar geometry without distorting the angles
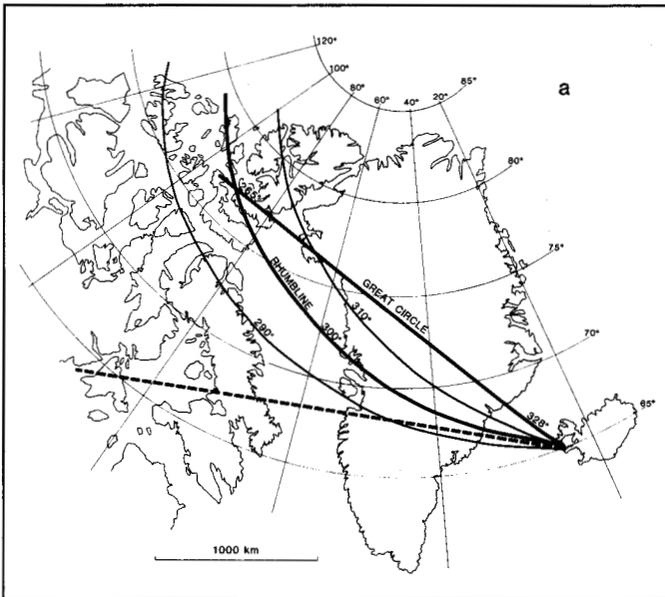
FIG. 7. Flight routes from Iceland towards N Canada according to different principles of orientation. a) Available data indicate that the main migration route runs close to the 300° rhumbline, with a large proportion of Knots, Turnstones and Brant Geese travelling in the indicated rhumbline sector 290-310°. This route is about 5% longer than the great circle route shown in the figure. The broken curve shows the route followed by birds departing from Iceland on a 300° bearing, using the sun compass for orientation without compensating for the time shift associated with the longitudinal displacement during the flight.
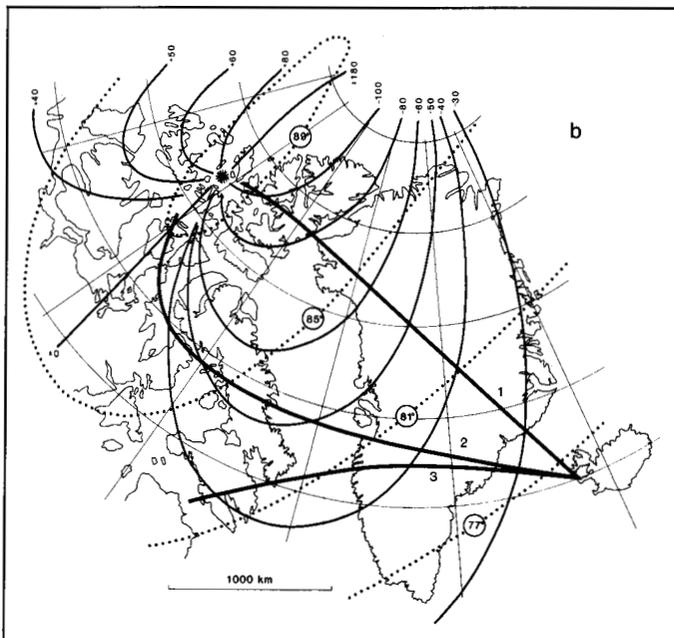
FIG. 7. b) Possible routes associated with magnetic orientation: (1) Route from Iceland to the north magnetic pole (indicated by star), with a constant magnetic course towards due north. (2) Route from Iceland with a constant magnetic course towards 324°. (3) Magnetoclinic route, according to the model by Kiepenheuer (1984). The latter two routes both have a 300° geographic departure course in W Iceland. Dotted and thin lines show the inclination and declination respectively of the geomagnetic field. Geomagnetic information (epoch 1985.0) for Canada and Greenland are derived from charts issued by the Department of Energy, Mines and Resources, Canada, and the Meteorological Institute, Denmark, respectively.

between longitudes. The implication of this is that birds could travel close to great circles at northerly latitudes by using their time-compensated sun compass (Emlen, 1975; Schmidt-

Koenig, 1979; Wiltschko, 1980-81), maintaining their internal clock in phase with time at the place of departure. Clock-shifting in birds, i.e., resetting their internal clock in phase with a shifted daily rhythm, normally takes at least four or five days (Schmidt-Koenig, 1979). One would therefore expect that the birds departing from Iceland have their internal clock in phase with daily solar time in Iceland throughout their long migratory flight, and only some days after arrival have they reset their internal daily rhythm in accordance with local time at the destination. Using the sun compass for orientation under these premises automatically results in a flight route closely resembling a great circle. By way of example, the great circle track shown in Figure 7a involves a total course change of 328 to 265°, or 63°. Using the sun compass as described above, the birds will follow a closely similar route with a total course change of 66°, which is equivalent to the longitudinal displacement (from 24° to 90°W).

(2) The north magnetic pole (NMP) is presently situated at about 77°N, 102°W in N Canada (Department of Energy, Mines and Resources, Canada, epoch 1985.0). Hence, by using their magnetic compass (Wiltschko and Wiltschko, 1988) and migrating on a magnetic course towards due north, the birds would follow an approximate great circle to the NMP (Fig. 7b). The great circle distance from W Iceland to the NMP is 2830 km, while the rhumbline route (towards 296°) is 206 km (7%) longer. The birds may reach other destinations in N Canada/NW Greenland by adopting constant magnetic courses slightly different from due north. Hence, the track following a constant magnetic course towards 354° represents a good approximation of the great circle shown in Figure 7a (with magnetic declination of 24°W in W Iceland, the initial geographic course along this track is 330°). Steep inclination angles and weak horizontal field intensities make the geomagnetic field difficult and unreliable to use for orientation in a wide area around the NMP. Whether birds can make use of their magnetic senses under these extreme geomagnetic conditions is an open question, but several studies indicate an acute degree of magnetic sensitivity in birds (Wiltschko and Wiltschko, 1988). Most days are magnetically disturbed in the Canadian Arctic. During moderate disturbances the daily track of the NMP keeps within an elliptic area about 50 km long, but during a severe disturbance the effective position of the NMP can shift between 80 and 160 km (Dawson and Dalgetty, 1966). Such disturbances would certainly cause large erratic course deviation for birds orienting by a magnetic compass sense but might still not render such an orientation mechanism useless.

Analyzing expected weather conditions en route, Alerstam *et al.* (1986) concluded that the great circle route from Iceland to N Canada/NW Greenland was less favourable and more hazardous than a detour a bit farther south, via the Disko region in W Greenland. Hence, weather rather than orientation difficulties probably provides the explanation of why the birds do not fly the shortest route between Iceland and their breeding destinations.

Let us now consider what mechanisms the birds could use to orient along the 300° rhumbline from Iceland (Fig. 7a). Long portions of this flight must occur over featureless sea or ice (Fig. 8). The fact that migrants depart not only at high cruising altitudes and in fine weather, but sometimes also at the lowest altitudes over the sea and with restricted visibility, suggests that other means of orientation than merely piloting with reference to landmarks are involved.
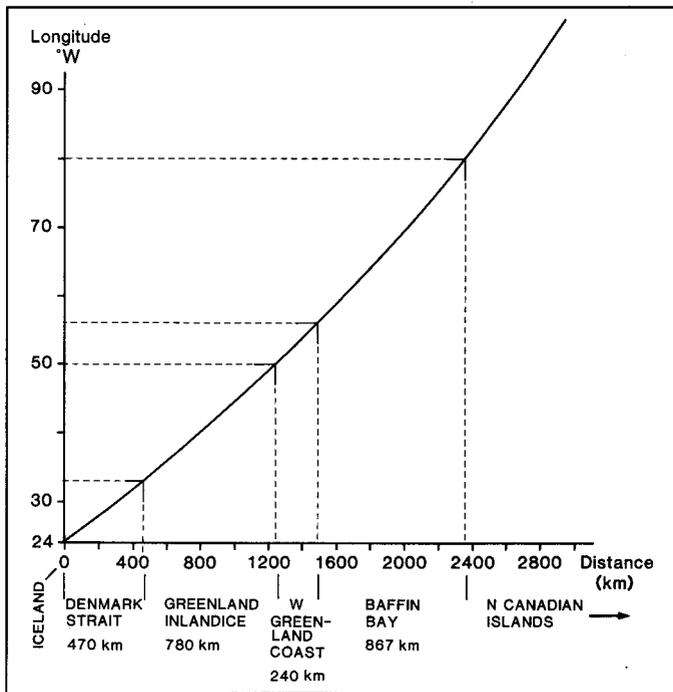
FIG. 8. Longitude versus distance along the 300° rhumbline route from Iceland to the Queen Elizabeth Islands in N Canada (cf. Fig. 7a). Passages across major expanses of sea, ice or land along this route are also indicated.

Birds using their time-compensated sun compass and departing towards 300° from Iceland will follow the route indicated by the broken line in Figure 7a. Only if they compensated for the time shift associated with the longitudinal displacement could they use the sun compass to follow the 300° rhumbline. This compensation must change during the flight as the birds cross longitudes at an increasing rate the farther to the north they get, as seen from Figure 8. Hence, with a flight speed of 60 km·h⁻¹, the migrants should, in order to keep a 300° geographic heading, start by adding 1.2° per flying hour to their sun compass course (operating in Iceland time), progressively increasing this rate of angular compensation to 2° or more per flying hour when approaching destinations in N Canada. The same effect will be achieved if the internal clock operating in the sun compass mechanism is slowed down from a circadian rhythm of 24 h under ordinary conditions to 26-28 h (overall average 26.6 h) during the actual flight.

With a magnetic declination of 24°W in W Iceland, the departure direction towards geographic 300° corresponds to a magnetic course of 324°. Extrapolating this magnetic course gives the route presented in Figure 7b. Obviously, this route is not used by the migrants, and we conclude that the birds do not migrate on a constant magnetic compass course.

Kiepenheuer (1984) suggested that migrating birds orientate by flying at a constant apparent angle of inclination, i.e., the inclination of the magnetic field vector as projected on a plane orthogonal to the bird's trajectory or body axis. With a magnetic inclination of 76.5° in W Iceland, the apparent angle of inclination for birds departing on a magnetic course towards 324° is 82°. The magnetoclinic route, along which this apparent angle is kept constant, is shown in Figure 7b. Again, this magnetic compass mechanism fails to explain the migration route of the birds.

CONCLUSION

The route used by the Knots, Turnstones and Brant Geese migrating from Iceland to N Canada/NW Greenland is now well documented on the basis of visual, radar and ringing data. Orientation conditions are extreme on this long-distance flight close to the geographic and magnetic north poles. This allows us to reject a number of different possible mechanisms of solar and magnetic orientation by the birds. The extensive knowledge available in the field of animal orientation seems to offer no reasonable explanation of how the birds manage to orient close to the 300° rhumbline route.

An interesting parallel is offered by Knots and Brant Geese performing a long-distance flight well over 4000 km from the Wadden Sea to the Taymyr peninsula in Siberia. Although the great circle route is about 400 km shorter and possible to follow, at least roughly, by using the sun compass as described above, the birds instead migrate approximately along the rhumbline route towards 60° (cf. Dick *et al.*, 1987).

Of course, the migrants could use a more complicated orientation program, changing their orientation at one or more intermediate points on their journey. The nature of the orientation system used by arctic migrants at northerly geographic and magnetic latitudes constitutes a highly fascinating and challenging problem.

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