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The Northward Migration of Arctic Waders in New Zealand: Departure Behaviour, Timing and Possible Migration Routes of Red Knots and Bar-tailed Godwits from Farewell Spit, North-West Nelson

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Summary: The departure behaviour of northward migrating Bar-tailed Godwits and Red Knots was studied on Farewell Spit, New Zealand, from 8–27 March 1994. Most flocks left in the evening and on rising tides. An exception occurred when waders responded to weather conditions favourable for migration, having had their departure delayed by strong winds for the previous five days. On average, flocks left with a slight tailwind, although some left with headwinds of up to 12 km h⁻¹. Most departures occurred after the passage of a low-pressure system or at the approach of a high-

pressure system, which produced favourable southerly winds. Despite observed departure directions being intermediate between those expected for flights to either northern Australia or northern New Zealand, most flocks probably encountered easterly winds from high-pressure systems and flew to Australia with some wind assistance. Varied assumptions of flight speed and the level of protein deposition show that flight range estimates can differ so widely that predicting migration routes is difficult.

Migrations of waders (Charadrii) have been the subject of much study over the past 30 years. Most information has come from the East Atlantic and the Western Hemisphere Flyways but there are few comparative data from other major flyways, such as the East Asia–Australasian.

The East Asian–Australasian Flyway extends from western Alaska and eastern Siberia at the northern extreme, down the Asian coast and through South East Asia to Australasia in the south. An estimated 4–6 million waders use this flyway in their annual migrations (Parish et al. 1987). New Zealand is situated at the southernmost extent of this flyway, and some 120 000 to 140 000 Arctic-breeding waders spend the non-breeding season there (P.M. Sagar pers. comm.). These are primarily Red Knots *Calidris canutus rogersi* (40 000 to 65 000; P.M. Sagar pers. comm.) and Bar-tailed Godwits *Limosa lapponica* (80 000 to 100 000). Of the five subspecies of knot currently recognised (Roselaar 1983; Tomkovich 1992) *C. c. rogersi* is one of the most poorly known (Davidson & Piersma 1992).

The Ornithological Society of New Zealand has conducted biannual counts throughout coastal New Zealand from 1983–94, so that knowledge of the distribution of coastal waders in New Zealand is now very good. However, information on movements within the country is lacking. Likewise, information about move-

ments between New Zealand and Australia is limited, although leg-flagging is proving very successful (Riegen 1995). From this we know that many knots pass through Victoria on the southward migration to New Zealand but not on the return journey north: Red Knots (hereafter referred to as Knots) from New Zealand are presumed to fly directly to northern Australia (A.C. Riegen pers. comm.). Irregular counts over the past 25 years from the far north of New Zealand (published in annual Classified Summarised Notes in *Notornis*) suggest waders may reach large numbers before departing on the northward migration. This raises the question of whether birds from the South Island as well as the North Island use the Far North before crossing the Tasman Sea.

Farewell Spit is situated at the north-west corner of the South Island and in summer holds large populations of Arctic waders. Birds there have three options: fly directly to Australia; fly to northern New Zealand, refuel, and then cross the Tasman Sea; or, possibly, fly directly to the east coast of China or Korea. Potential flights for the different options would be in the order of 900 km (Northland, New Zealand), 2500 km (east coast, Australia), 3900 km (Gulf of Carpentaria, northern Australia) or 8500–9000 km to Japan or Shanghai. In general, an initial heading should not be extrapolated to indicate probable area of destination (Piersma et al.

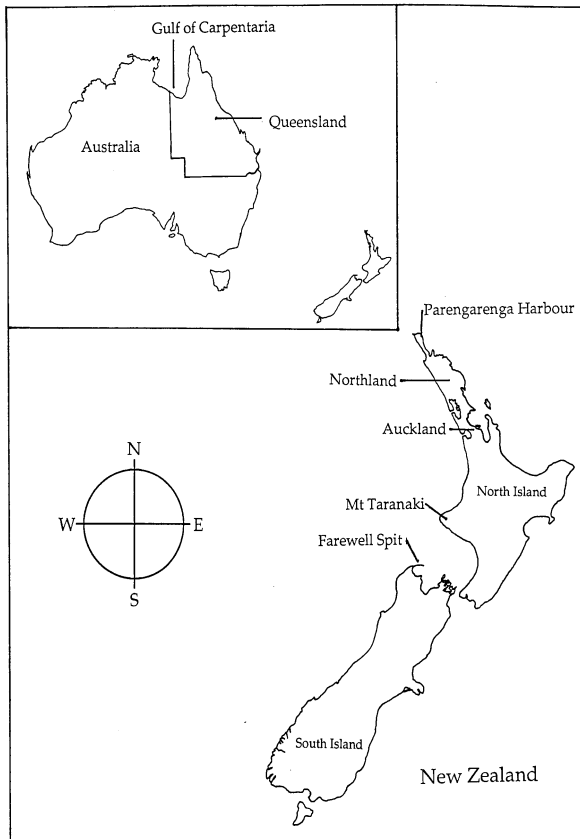


Figure 1 Map of localities in Australasia mentioned in the text.

1990b). Farewell Spit is, however, perhaps the one place in New Zealand where such inference is feasible. Being south-west of the North Island, the direction taken by waders leaving Farewell Spit might allow predictions about the destination. Given data on departure directions and potential flight ranges (based on body mass and nutrient stores at departure) possible migration routes could be constructed (e.g. Tulp et al. 1994).

This paper examines the departure behaviour of migrating waders, a field which has been fruitfully studied in the northern hemisphere (e.g. Lank 1989; Alerstam et al. 1990; Piersma et al. 1990a; Piersma et al. 1990b). The aim is to combine observed departure directions with information on contemporary weather systems to detect whether waders on Farewell Spit migrate directly to Australia. Using data on mass change in Knots from northern New Zealand (Battley

1996; Battley & Piersma 1997), potential flight ranges of knots are calculated under a variety of constraints (too few data exist to allow this approach for Bar-tailed Godwits, hereafter referred to as Godwits), and the migration strategy of New Zealand-wintering Knots is discussed.

Methods

Observations of migrating Arctic waders were made from near the tip of Farewell Spit, Golden Bay, New Zealand ($40^{\circ}33'S$, $173^{\circ}01'E$; Fig. 1) during March 1994. Intensive watches were made from small knolls (c. 3 m high) overlooking tidal flats for around three hours before dusk each night, the time when most flocks are likely to depart (Lank 1989; Piersma et al. 1990b). However, I was in the field over much of the day (Fig. 3) and the departures of only a few flocks at other times are likely to have been missed. An area of up to 10 km^2 at low tide was scanned with 10×40 binoculars and flocks were followed with a 25×60 telescope. Any migration activity was noted whenever I was on the sandflats during the rest of the day.

When a flock of departing waders was observed the following details were noted: species, number of birds, time, flock flight formation (after Piersma et al. 1990b: bunch, cluster, vee and echelon, and transitions between these), whether the sun was visible and whether flocks were vocalising. Whenever possible the flight direction of migrating flocks was determined by compass. If a flock passed more than about 300 m away, no direction was recorded to avoid substantial parallax problems.

When departing flocks were observed, an estimate of ground wind speed in 5-knot intervals was made (based upon experience gained during regular reading of the anemometer at the Farewell Spit lighthouse over the previous four months). Wind speed usually varied little throughout the course of an evening and the anemometer on the lighthouse was normally checked both before and after an evening watch. In addition, wind direction was noted in one-eighth compass directions (e.g. NW, W, SW, etc.). With the wind speed and direction, and bird speed (assumed to be 65 km h^{-1} although when climbing this may be expected to be lower) and direction known, the wind effect can be calculated. The formula for calculating the wind effect (from Piersma & Jukema 1990) is:

$$\Delta W = W * \cos a + \{A^2 - (W * \sin a)^2\}^{0.5} - A$$

where W is the wind speed (km h^{-1}); a is the angular difference between the track (t , departure direction of

birds) and the wind direction (w), so $a = w \pm 180^\circ - t$; and A is the bird's air speed (taken as 65 km h^{-1}). A positive wind vector is referred to as a tail-wind, and a negative vector a headwind.

A generalised synoptic weather map was used to plot where departures occurred relative to major weather systems at that time. This approach has been successfully used in the northern hemisphere for migrating waders (e.g. Richardson 1979; Lank 1983). This gives a static frame of three pressure systems and associated fronts, and wind directions. My map is a reversal (for southern hemisphere conditions) of the one used by Richardson (1979) and Lank (1983). In these maps, the land moves relative to fixed weather systems, rather than the other way around. This allows an aggregate picture to be formed of the way in which birds respond to large-scale weather conditions (in contrast to local conditions detailed above). Daily weather maps were taken from the *Dominion* newspaper during March 1994. The position of the NW South Island relative to the generalised weather systems was estimated from these maps and actual conditions at departure.

In addition to computing the standard arithmetic mean flock size ($\sum x/n$), the mean flock size as experienced by the average bird ($\sum x^2/\sum x$) was also calculated. In effect, this method weights the flocks according to their size, so the number of birds experiencing a given flock size is accounted for in the analysis (Piersma et al. 1990b).

Potential flight range estimates for Knots in New Zealand were calculated using four predictive methods: Summers & Waltner (1978), Davidson (1984), Castro & Myers (1989) and Pennycuick (1989). Many studies of waders have assumed a flight speed of 75 km h^{-1} (e.g. Thomas 1987; Castro & Myers 1989; Barter & Wang 1990), while others suggest this may be too high (Alerstam et al. 1990; Zwarts et al. 1990; Gudmundsson 1993). Therefore, speeds of 75 km h^{-1} and 65 km h^{-1} were used (except for Pennycuick's method, which calculates its own maximum range flight speed). Some of the premigratory mass increase in birds can consist of protein, while equations treat it as being solely fat (Piersma 1990; Lindström & Piersma 1993). Protein provides only one eighth the energy of fat (Piersma & Jukema 1990), so these estimates need to be devalued accordingly. It is probable that both supplies of protein and fat in the bird oscillate in tandem, with protein becoming exhausted as well as fat (T. Piersma pers. comm.). For the purpose of this analysis I regarded protein as being used constantly through the flight, and not

kept in store until fat reserves run out. This does not affect the pattern of weight loss assumed in the above methods. Assuming that (for example) only 70% of the increase is due to fat, and 30% to protein, the energetic 'worth' of the reserve becomes 70% of (fat) reserve times 100% energy, plus 30% of (protein) reserve times 12.5% energy, giving a factor of 0.7375, which is then multiplied by the original flight range estimate. Calculations for protein levels of 0.3, 0.2 and 0.1 have been calculated in this fashion for Knots. A lean mass was taken as 109 g and departure mass as 185 g (Battley & Piersma in press, data on body composition of 15 Knots from northern New Zealand).

Circular statistics follow those of Batschelet (1981).

Results

Premigratory and migratory behaviour

Conspicuous 'pre migratory' flights were largely lacking. The first evidence of premigratory restlessness was shown by 13 birds on 5 March. These flew eastward over the tidal flats parallel to the land for about 4 km, slowly gaining height, before turning around, flying westward and returning to ground, having flown at least 8-9 km in five minutes. Most departing flocks were located after they had flown from distant tidal flats: only six actual lift-offs or pre-flight behaviours were noted. Birds involved in one of the first flocks of Knots to depart, 25 birds on 8 March, were conspicuous on the ground beforehand. In a flock of 990 roosting birds facing into the wind, about 26 birds in very strong breeding plumage walked through the flock, calling. These calls were mainly a characteristic clear *huit-huit-huit*, but also included a low chucking that can be heard from feeding birds (PFB pers. obs.). There was also a *ke-ke-ke*, on the same note. Over the next hour several groups (of 43, 44, 6, 8, 5, 4 and 6) flew away from the main flock, calling as they went, but settled again 200 m away and were not seen to migrate before dark. Eventually, a flock of 28 birds flew of which three birds returned to the ground after two minutes, but the rest migrated. The breakaway groups began feeding, despite the high tide, and eventually all but 160 Knots were feeding. This unusual high-tide feeding may have been induced by premigratory restlessness, by disturbance by an Arctic Skua *Stercorarius parasiticus* (feeding is often a displacement activity for disturbed roosting waders: PFB pers. obs.), or by a neap tide that left some feeding habitat still exposed. Equally conspicuous be-

Table 1 Flock sizes, vocalisation and presence of visible sun at departures for Red Knots and Bar-tailed Godwits, at Farewell Spit, March 1994. Arithmetic mean flock size is $\Sigma x/n$, while the average bird flock size is $\Sigma x^2/x$, where x is flock size.

	Flock size:		Vocals			Sun	
	arithmetic mean	average bird	Yes	No	?	Yes	No
Red Knots	33.7	40.3	15	0	—	7	8
Bar-tailed Godwits	40.4	53.0	16	2	9	10	17

behaviour was shown by Godwits on 19 March, with small groups of noisy birds taking small flights away from a roosting flock, and then not dispersing out to the tidal flats as they became exposed. Eventually, only the separated non-feeding flock was left near the shore and they departed soon after.

A total of 42 separate flocks of wader (15 Knot, 27 Godwit) was recorded, totalling 1581 birds (491 Knot, 1090 Godwit). All but two flocks were monospecific, the exceptions being three Knots each time flying with flocks of 27 and 48 Godwits respectively (for analysis the Knots in these flocks have been ignored). Flock characteristics are given in Table 1. Godwit flocks ranged from 8-110 birds and Knots from 13-75, but the difference in mean flock size (arithmetic) was not significant ($t_{38} = 1.16$).

Most flocks of Knots and Godwits were recorded vocalising (Table 1). A visible sun was clearly not required for migration (Table 1).

Many flocks appeared to require some time to settle on their departure direction, and would proceed in a series of small zig-zags, similar to behaviour noted for Knots elsewhere (Swennen 1992). Flock structure also changed during the first few minutes of flight, with flocks tending to 'evolve' to an echelon or vee (Table 2). There is also the suggestion from Table 2 that Godwits achieved an ordered flock formation sooner than Knots. This could have resulted, though, from Godwits leaving mainly from the tideline, whereas Knots were often spread over the tidal flats.

Patterns of departures

The daily pattern of observed departures is shown in Figure 2. While the last recorded departing flocks were on 27 March, there still remained small numbers of Knots in breeding plumage, which suggests that they were going to migrate that season (Zwarts et al. 1990). However, as many of these birds were still present after the first week in April, it is possible that these birds re-

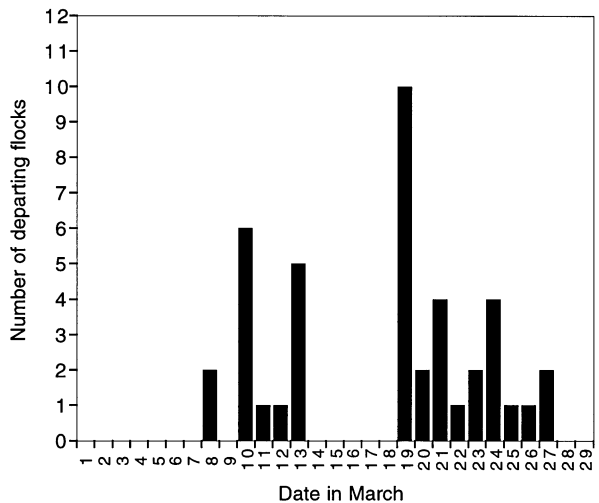


Figure 2 Daily pattern of observed departures of knot and godwit from Farewell Spit, March 1994.

Table 2 Departing flock formation and changes in Red Knots and Bar-tailed Godwits at Farewell Spit, March 1994. Categorisation of flocks follows Piersma et al. (1990a). A cluster was a group of birds with no obvious flock structure; a vee was formed by two lines of birds trailing a single leader; an echelon (ech) was a straight line of birds. (The latter two were not always distinguishable.)

	Cluster	Cluster-Vee/ech	Vee	Vee-ech	Echelon	Cluster-Vee-ech
Red Knots	4	9	2	—	—	—
Bar-tailed Godwits	—	12	9	4	1	2

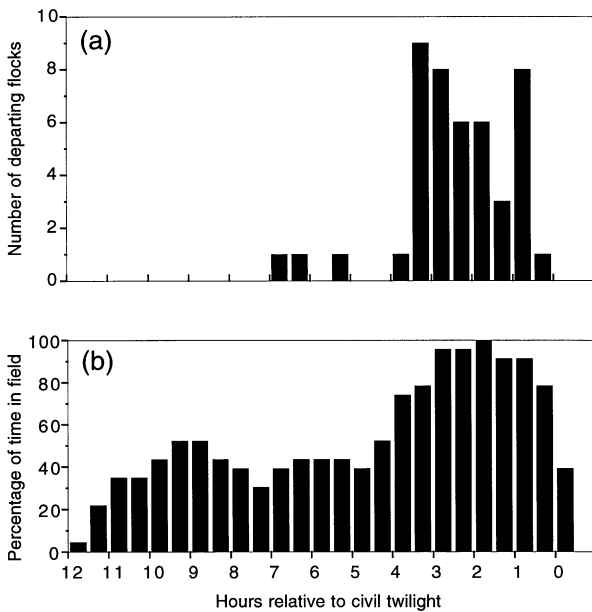


Figure 3 Pattern of departures relative to time of day (a) and observer time in field (b).

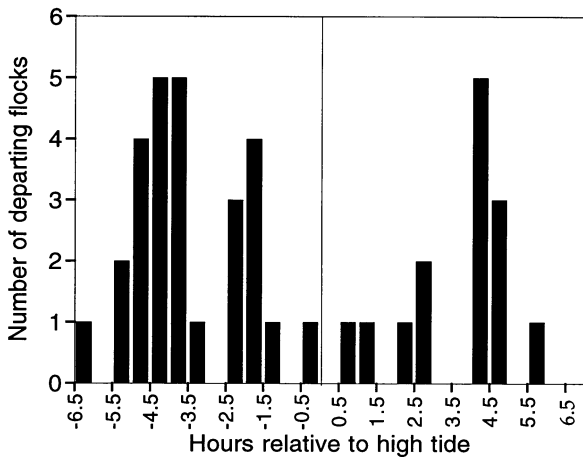


Figure 4 Pattern of observed departures relative to tidal stage. Zero denotes high tide (vertical line). X-axis increments are half-hour intervals.

mained on the spit, or at least in New Zealand. Barter et al. (1988) showed that many first-year Knots enter breeding plumage. However, the Knots recorded by Barter et al. (1988) reached only weak breeding plumage, in contrast with this study, where the Knots

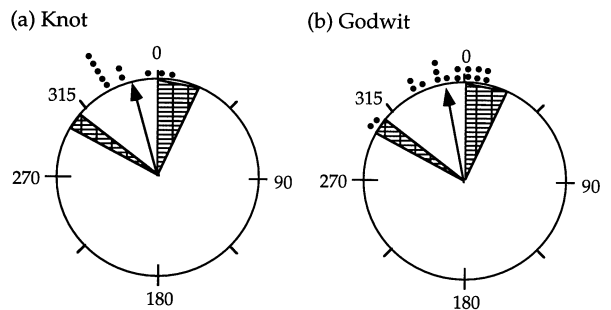


Figure 5 Directions of departures for knot and godwit. Dots on the outside of the circle represent flocks for which accurate compass bearing were gained. Flocks are in 5° groups. Mean departure vector and length (r) is given as an arrow from the centre of the circle. Hatched sectors show directions to northern Australia and northern New Zealand.

were in virtually full breeding plumage. Second-year birds are likely to be more strongly plumaged than first-years and it appears that many second-year birds do remain in New Zealand over the southern winter (New Zealand Wader Study Group unpubl. data). It is possible that these strongly-plumaged birds were second-years, or even adults. The lack of departures from 14–18 March was probably owing to constant strong headwinds over that period (see below).

Most flocks departed in the evening (Fig. 3), with the majority of flocks departing on a rising tide (Fig. 4). There is the suggestion of a bimodal pattern, with peaks around mid-tide on both rising and falling tides. However, on 19 March (following the period with no departures) nine of ten flocks departed in the evening during the falling tide. Because their departure had been delayed by the weather (see below) the falling tide probably had no influence on their departure. If these flocks are omitted from the analysis, the influence of a rising tide becomes stronger.

Direction of departures

Compass directions were obtained for 17 Godwit flocks and ten Knot flocks (Fig. 5). Mean departure vector (track) for Godwits was 350.3° (mean vector length $r = 0.944$) and for Knots 344.6° ($r = 0.974$), but these differences were not significant (Watson–Williams test, $F_{1,25} = 0.92$; ns). Mean heading direction was also calculated (the heading being the direction a bird actually attempts to fly). This was calculated by adding the track direction vector (the course achieved in the influence of wind; I assumed 65 km h⁻¹ ground speed) and the wind

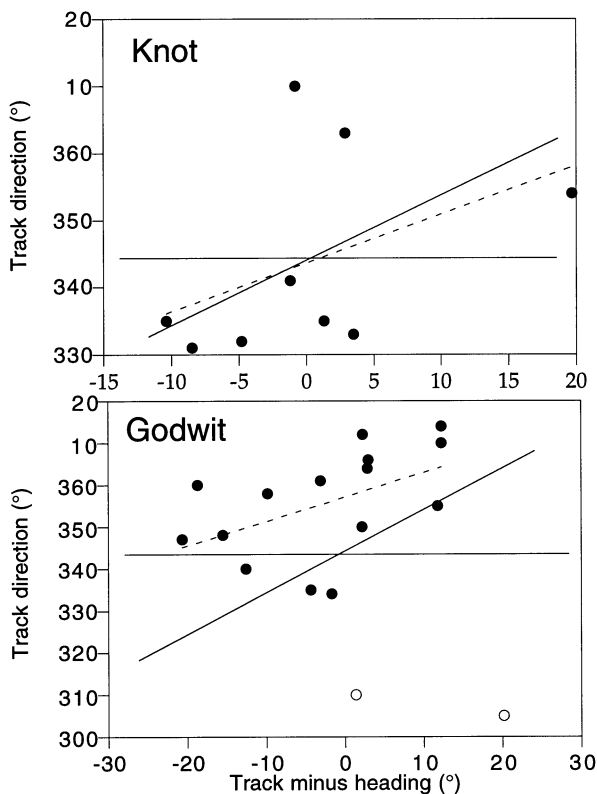


Figure 6 Degree of wind drift experienced by departing flocks. The track direction is the observed departure direction. The heading is the direction birds attempted to fly. The difference between the two is the wind effect. The heading was determined by adding the bird and wind vectors, assuming a ground speed of 65 km h⁻¹. The relationship between track minus heading and track, shows a slope of zero if there is complete compensation for winds and a slope of one if there is complete wind drift (solid lines). The dotted line shows the regression for the data. The two hollow points in the godwit plot were removed from the analysis (see text).

vector (which also has a direction and speed). Mean heading for Knots was 343.6° ($r = 0.954$; $n = 9$ in this case because, for one flock, no wind details were recorded) and for Godwits it was 352.0° ($r = 0.924$).

Whether birds compensate for winds can be determined by regressing the birds' track direction on the track minus heading direction (Alerstam 1976, cited in Piersma et al. 1990b). A slope of one for the relationship indicates complete wind drift, while a slope of zero indicates total compensation (solid lines in Fig. 6). Great variability was shown within both species (Fig. 6) and Knots showed a positive relationship (slope =

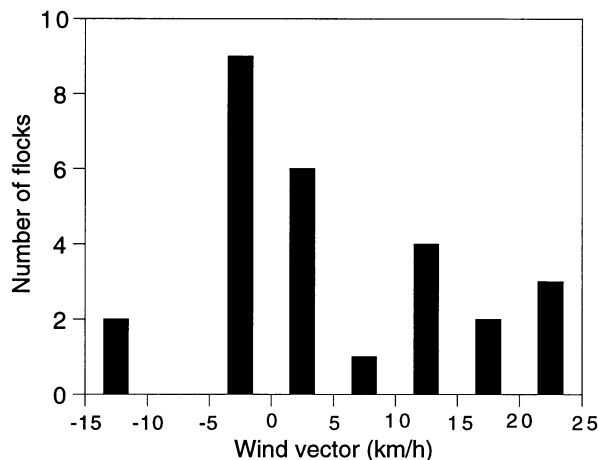


Figure 7 Wind vectors for departing flocks. A positive wind effect is a tailwind, a negative wind effect a headwind. See text for explanation.

0.726, $r = 0.43$, $P = 0.246$), Godwits a flat one (for all data points, slope = -0.099 , $r = 0.06$, $P = 0.827$). However, when the two outliers in the Godwit plot were removed from the analysis (hollow circles in Fig. 6) then an almost significant positive relationship emerged (slope = 0.582, $r = 0.49$, $P = 0.063$).

Influence of weather

For 26 flocks for which full details were gathered, wind vectors at departure ranged from a tailwind of up to 22 km h⁻¹ to a head wind of up to 12.8 km h⁻¹. The modal range was -5 to 0 km h⁻¹ (Fig. 7), but the mean wind effect for all 26 flocks was a 3.9 km h⁻¹ tailwind.

Winds on Farewell Spit are variable, and frequently strong. From 14–18 March, birds faced north-westerly winds of generally 15–20 Knots (28–37 km h⁻¹) at sea level. During this time no flocks were seen to depart and no obvious premigratory restlessness was observed, so probably no birds departed. Taking a mean departure track of 347° and a flight speed of 65 km-h, the calculated wind vector for birds attempting to migrate into a NW wind of 32 km h⁻¹ is -29.4 km h⁻¹. Hence, if the winds at sea level were at all similar to higher altitude winds, then birds' airspeed would be virtually halved in such conditions. The lack of migratory behaviour from 14–18 March, combined with the large numbers of departures on 19 March (Fig. 2) indicates that migration was suppressed over the former period. When conditions became favourable again (winds on the evening of

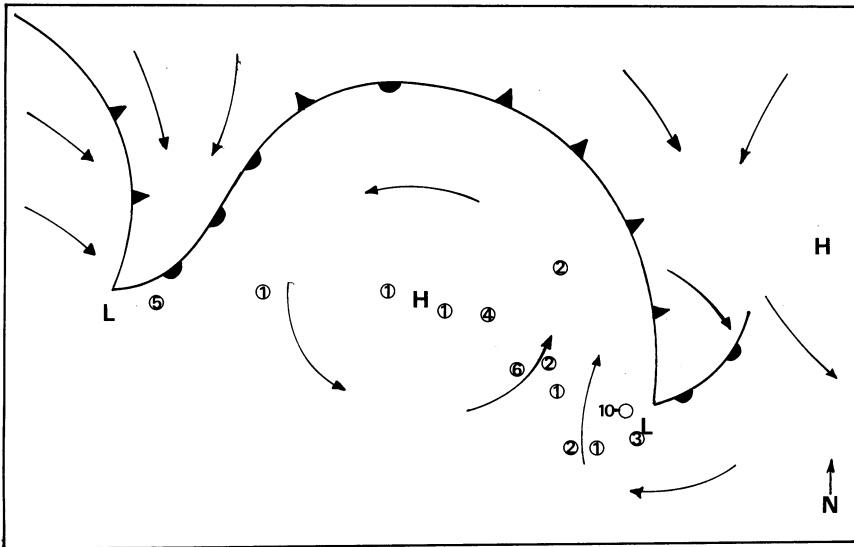


Figure 8 Plot of departure occurrences relative to prevailing weather systems. H = high pressure, L = low pressure. Arrows show wind directions. Each circle represents a day on which flocks departed. The number inside the circle shows how many flocks were seen.

19 March were south-easterly at 15-20 Knots) a larger than normal cohort was physiologically ready to migrate.

The weather systems prevailing over the period 14–18 March showed clearly why migration was suppressed: a large slowly moving low pressure system centred over the mid-Tasman Sea caused prolonged north and north-westerly winds to occur. This moved south-east below New Zealand on 17 March and a new low developed just west of the northern South Island and moved east over the country on 19 March, bringing with it south-easterly winds suitable for migration. The position of days on which flocks departed relative to major weather systems is plotted in Figure 8. The majority of flocks departed after the passage of a low-pressure system or with the approach of a high-pressure system.

How far might Red Knots from New Zealand be able to fly?

The predicted flight ranges for Knots in Figure 9 show that there is great variability in the estimates depending on both assumed level of protein deposition and flight speed. Under Pennycuick’s model, Knots would be unable to fly to Australia unless their mass increase consisted of 90% fat. Under all other models, flying at 65 km h⁻¹ Knots could travel at least 3000 km and reach Australia, but not reach the Gulf of Carpentaria unless 80% to 100% of their mass increase was fat. At 75 km h⁻¹, all but Davidson’s and Castro & Myers’s models at

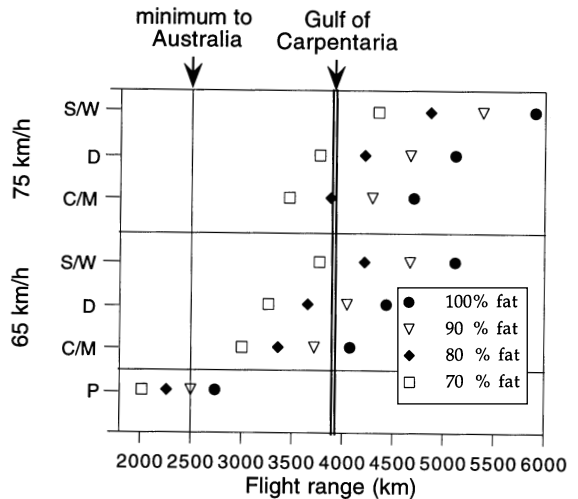


Figure 9 Estimated flight range of knots. Four predictive methods were used: S/W = Summers & Waltner (1978), D = Davidson (1984), C/M = Castro & Myers (1989), P = Pennycuick (1989). Flight speeds of 75 km h⁻¹ and 65 km h⁻¹ were used for the first three methods: Pennycuick (1989) calculates its own maximum flight speed (49 km h⁻¹). The four estimates for each method show different levels of fat deposition (see text): filled circles = 100% fat, hollow triangles = 90% fat, filled diamonds = 80% fat, hollow squares = 70% fat. Vertical line gives the minimum distance from New Zealand to Australia, the double vertical line from New Zealand to the Gulf of Carpentaria, northern Australia. Variables used were lean mass 109 g, departure mass 185 g (Battley 1996; Battley & Piersma in press), wingspan 47.5 cm (Tulp et al. 1994), wing length 16.75 cm (NZWSG unpubl. data, n = 1871).

70% fat could reach the Gulf of Carpentaria. (Note that these models assume zero wind effects at the migration height.)

Discussion

Migratory behaviour

Flock sizes of migrating waders show large differences between localities. The average flock size of Godwits on Farewell Spit was considerably lower than that of north-western Australia (Tulp et al. 1994) and the Banc d'Arguin, Mauritania (Piersma et al. 1990b), but was only slightly less than that of The Netherlands during the northward migration (Piersma et al. 1990b). Knot flocks were similar in size to those departing from Roebuck Bay, north-western Australia (Tulp et al. 1994) and the Banc d'Arguin, Mauritania, but much smaller than those from the Dutch and German Wadden Sea (Piersma et al. 1990b; Swennen 1992). Given a limited pool of individuals, of which only some may be physiologically ready to migrate, differences in migrating flock size could relate to the local population size. Piersma et al. (1990b) showed that mean flock size for Godwits and Knots departing from Mauritania was larger during peak departure times (the ten-day period during which most flocks left).

There are, unfortunately, few data with which to test this assertion. On Farewell Spit, the local flocks of Knot and Godwit were each around a thousand birds. Tulp et al. (1994) recorded only up to 2000 Knots in their study area in north-western Australia during the migratory period and had flock sizes only slightly larger than those at Farewell Spit, which is consistent with this hypothesis. While numbers of Knots wintering on the Banc d'Arguin are vast (c. 362 000: Piersma et al. 1992), the relevant factor is the size of the local population immediately before to migration, particularly those on tidal flats. Lank (1983) found differences in flock sizes of migrating Semipalmated Sandpipers *Calidris pusilla* migrating from Kent Island, Bay of Fundy, and from Sibley Lake, North Dakota (with oceanic flocks at the Bay of Fundy being larger than overland flocks in North Dakota), but found no significant correlation between local population size and flock size. Instead, he concluded the differences may have arisen from differential selection pressures on flock size in coastal and inland sites, owing to prevailing weather conditions (e.g. navigational and/or aerodynamic factors). While all the sites mentioned above for Godwits and Knots

are coastal, they presumably experience different weather conditions, given that some are temperate and some are tropical. However, as differences in flock size have been recorded for sites along the same flyway (Piersma et al. 1990b) used by the same populations (Banc d'Arguin and the Netherlands; Dick et al. 1987; Piersma & Jukema 1990), differences in flock sizes here may reflect some local departure-specific factor (or factors) rather than a basic underlying difference, as in Semipalmated Sandpipers.

The tendencies of birds to vocalise strongly, evolve flock structure towards a vee or echelon and to have apparent difficulty in settling on a final course, have been well documented (Piersma et al. 1990b; Swennen 1992). The zig-zagging of flocks setting off could be caused by them both attempting to settle on a course, and to trying to maintain that course in crosswinds.

Timing of departure

Since Lank (1989) published his thought-provoking results on the timing of shorebird migration, much interest has focused on clarifying the effects of time and tide on migration of waders (Alerstam et al. 1990; Piersma et al. 1990b; Marks & Redmond 1994; Tulp et al. 1994). The pattern emerging is that with an increase in tidal amplitude, there is an increase in the influence of a rising tide on departures. Departures from Farewell Spit (tidal range 2-4 m) seem also to conform to this pattern, with most departures on a rising tide. Tulp et al. (1994) calculated a 'tidal influence index', which confirmed the influence of tidal range on departures, with sites that had a larger tidal range in general having a larger tidal influence index.

However, the way in which the data were treated means that their index does not actually relate to tide as such. What is important is whether more departures or fewer departures than expected occurred for a given part of the tidal cycle. Because Tulp et al. (1994) summed the absolute differences between observed and expected frequencies of departures (i.e. ignoring the sign), this information is lost. A similar index could be calculated for distributions in which the departures oscillated through the tidal cycle, and one in which all departures occurred on an incoming tide (Fig. 10). Therefore, instead of measuring a specified *tidal* effect, what is measured is how much overall variation there is through time. The amplitude of the variations would determine the level of the index.

If the signs of the deviations are considered over specified parts of the tidal cycle (incoming/outgoing,

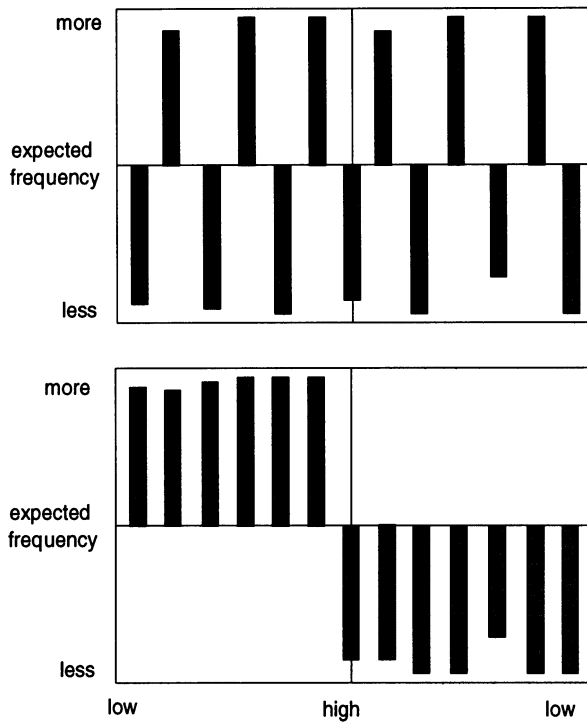


Figure 10 Schematic representation of two hypothetical distributions of migratory departures according to tidal stage. In the first, departures oscillate with no relation to tide. In the second, all departures occur on an incoming tide. If the sign of the deviations is ignored, then the Tidal Influence Index for the two would be identical. When the signs are included (and deviations summed for incoming tides, for example) then the oscillating distribution receives an index of roughly zero. The distribution with departures on the incoming tide receives a positive index.

the hour around high tide being combined with outgoing tides), then a measure of the coarse effects of tide can be generated. I have calculated a new 'tidal influence index' in which the difference between the observed frequency distribution of departures and the expected frequency distribution (departures spread equally among time periods: $\sum \text{departures}/13$) is calculated for each part of the tide. This is then summed (retaining positive or negative sign) for the incoming and outgoing tide periods. A positive sign indicates more departures than expected for that part of the tidal cycle; a negative sign fewer. (As all the deviations combined will equal zero, the outgoing tide index will equal the incoming tide index, but with an opposite sign.) The absolute magnitude of the number then becomes the in-

dicator of how strong this effect is: the larger the index, the greater the deviation from expected.

Figure 11 plots this tidal influence index for incoming tides. Two points are given for Farewell Spit. The smaller is based on the complete data set and the larger on the set minus all departures on 19 March, when birds were migrating apparently in response to favourable weather conditions. The influence of incoming tides appears to increase with tidal amplitude.

However, the relationship is not simple. At Roebuck Bay, which has a high tidal range (Fig. 11), many waders departed on the outgoing tide. This was due to a tidal cycle in which high tides usually fell in the middle of the day. Departures on the outgoing tide were therefore in response to time of day effects (i.e. in the pre-dusk period). The majority of departures on the outgoing tide on Farewell Spit also appeared to be in response to time of day, combined with suitable winds

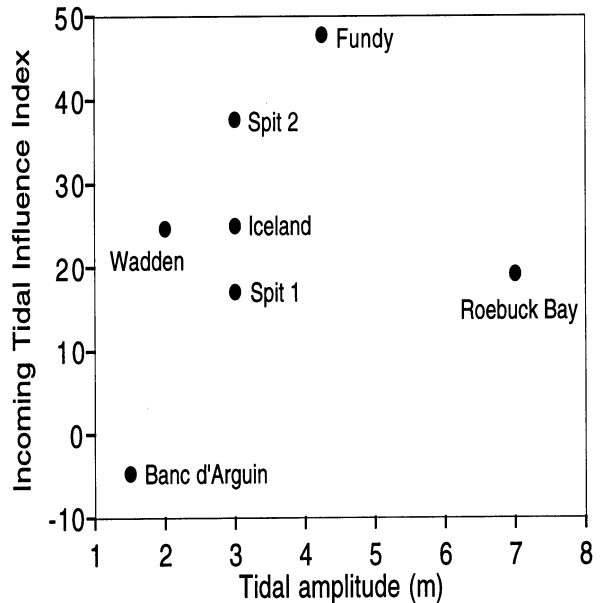


Figure 11 Tidal Influence Index, plotted against tidal height. The y-axis represents the deviation from a uniform pattern of migratory departures over the whole tidal cycle. A positive value shows more departures occurred on an incoming tide than outgoing. The magnitude of the index indicates how strong the tidal effect is, in either direction. Abbreviations and source of data: Banc d'Arguin (Piersma et al. 1990b); Fundy = Bay of Fundy (Kent Island: Lank 1989); Roebuck Bay = NW Australia (Tulp et al. 1995); Iceland (Alerstam et al. 1990); Farewell Spit 1 and Farewell Spit 2, this study (see text).

(see below). The few departures on outgoing tides recorded by Lank (1983) were in response to favourable weather conditions.

Disturbance by moving water might trigger birds to migrate (Piersma et al. 1990b; Gudmundsson & Lindström 1992; Tulp et al. 1994). In this study many flocks formed away from the tidal edge, so this explanation could not relate to them. Thus, I cannot accept an incoming moving water front as being any more than a partial explanation.

The feeding priority hypothesis (Lank 1989), proposes that waders migrate on the incoming tide in order to maximise potential feeding time prior to this. Staying over high tide, when feeding is impossible, has no energy benefit, so departures are concentrated on the incoming tide. Lank (1989) suggested this was important for coastal Semipalmated Sandpipers in the Bay of Fundy. Departures of Knots and Godwits from Farewell Spit appear to fit this model, probably interacting with time of day effects.

The diurnal effect on timing of departure of birds from Farewell Spit was pronounced, as for other migrating waders (Lank 1989; Alerstam et al. 1990; Piersma et al. 1990b; Gudmundsson 1993; Tulp et al. 1994). The tendency for evening departures may be due to a complex array of potential flight and navigational benefits (Piersma et al. 1990b), including skylight polarisation patterns (that vary according to the position of the sun), stars and sun. While waders at both the Banc d'Arguin and the Netherlands departed in sight of a setting sun, the majority of flocks from Farewell Spit were unable to do so (although the sky was sometimes visible). Where the sky was visible, skylight polarisation patterns could have been used.

Effect of weather

Most flocks departing from Farewell Spit gained from wind assistance. Birds were obviously sensitive to local weather conditions and did not migrate in strong headwinds. While I have no data on winds at higher altitudes, which can differ from those at ground level (for example, see Piersma & van de Sant 1993), Figure 8 shows that birds departed when large-scale weather systems were favourable for migration. This suggests a strong relationship between local and large-scale weather conditions, in contrast with the study of Piersma et al. (1990a) in tropical Mauritania, in which the intensity of migration was not correlated with ambient wind circumstances (as ambient wind circumstances themselves were uncorrelated with higher-altitude

winds). The results from Farewell Spit are, however, in accord with temperate northern hemisphere studies (Blokpoel & Richardson 1978; Richardson 1978; Richardson 1979; Lank 1983) in which favourable winds behind a cold front were used for migration.

Despite this purported sensitivity to wind conditions, birds were not seen making extensive 'pre-migration flights' during which birds would have the opportunity to assess windspeeds. That birds were not doing so implies that they either had already 'decided' whether to migrate on the basis of winds experienced earlier in the day (e.g. when feeding on the tidal flats) or that they could fairly accurately assess windspeed independent of their own flight.

Flight ranges

The usefulness of flight range estimates is open to dispute, as they are subject to many sources of error (Zwarts et al. 1990). Until recently, all of the premigratory increase in mass in birds was assumed to consist solely of fat, with protein levels maintaining a constant 'structural' level. A sizeable portion of this mass increase can, however, consist of protein (Piersma 1990; Lindström & Piersma 1993), but flight range equations are based on flight metabolism using only fat. Increasing protein deposition would decrease predicted flight ranges. Waders are assumed to adjust their flying altitude to maximise tailwind assistance (or minimise headwind hindrance), while flight range equations assume no wind effects. This would, in most cases, tend to increase predicted ranges. Other factors affecting flight range estimates are energetic savings by flock flying, which would increase distance, and the actual flight speed. Most studies have used a flight speed of 75 km h⁻¹ for waders but 65 km h⁻¹ may be a more realistic estimate (see Piersma et al. in press). Nevertheless, flight range estimates have been widely used and allow first estimates of magnitude of potential flights and comparison between populations and areas.

This study formally accounted for protein deposition and different flightspeeds in estimating flight ranges. Varying protein levels resulted in differences of up to 1549 km (Summers & Waltner method, 75 km h⁻¹) and varying flightspeed from 75 km h⁻¹ to 65 km h⁻¹ gave a maximum difference of 787 km (Summers & Waltner method). Obviously, both these variables can greatly affect flight range estimates, so without either detailed information on levels of protein deposition (Lindström & Piersma 1993) or details of winds en route (Piersma & Jukema 1990; Piersma & van de Sant

1992; Tulp et al. 1994), any predictions will be subject to potentially large errors.

I used a lean mass of 109 g that was derived from body composition of premigratory Knots from northern New Zealand. Other workers (Barter 1992; Tulp et al. 1994) have used a much lower estimate of 87-88 g, which represents the body mass of newly-arrived migrants showing depleted body masses. They had probably used both fat and protein reserves (which differ from nutrient stores deposited before migration: see Lindström & Piersma 1993; van der Meer & Piersma 1994), so treating the difference between this mass and departure mass as being just fat is inappropriate and will result in inflated flight range estimates.

Do Red Knots fly to Australia direct or via Northland?

Through banding records and, recently, leg-flagging, some information about movements of Knots within Australasia is known. Some Knots travelling to New Zealand use south-eastern Australia on the southward migration but do not use this area in the northward migration (Barter 1992). However, there are records of Knots from New Zealand in south-eastern Queensland and Irian Jaya, and it is probable that the Gulf of Carpentaria is extensively used on both migrations (Barter 1992). Alcorn et al. (1994) suggest, however, that birds arriving on south-eastern mudflats in January to February could have been from New Zealand, although it is possible that this involves birds still moving south within Australia. The destination for Knots leaving New Zealand on the northward migration is presumably northern rather than south-eastern Australia and the Gulf of Carpentaria is probably the only regular stop for Knots flying north through Australia (A.C. Riegen pers. comm.).

It was anticipated that migrating Godwits and Knots would show a clear distinction in departure flight path that would indicate whether they were flying direct to Australia from Farewell Spit or were staging in northern New Zealand. Birds leaving the spit have a clear and visible landmark in the form of Mt. Taranaki (39°18'S, 174°04'E), 190 km away at 50° from the spit. Birds flying to the Auckland isthmus area would require a course holding 25°, while a course of 359° would place birds at Parengarenga Harbour in Northland. A constant compass bearing course (Rhumblin) to the Gulf of Carpentaria, northern Australia, would be 309°, while the great circle course would depart at 299°.

The recorded compass bearings for Godwit and Knot flocks from Farewell Spit seem too far east for a direct flight to Australia, unless they encounter a predictable easterly wind stream en route. On ten of the 13 departure days migrating birds would have been able to fly into or across the top of a high pressure zone, thus getting assistance from easterly winds. Parallel isobars frequently indicated a windstream that would extend from the southern North Island to the Queensland coast. The fact that flocks were not compensating for wind drift accords with a relationship with large-scale weather patterns — predictably changing wind patterns (e.g. around a high-pressure system) could mean that fine-tuning migration directions might not be necessary until further on in the trans-Tasman flight. For the remaining three days, to encounter southerly wind flows would have required flying across a low pressure system (eight flocks totalling 178 Godwits [16% of the total individuals] and 56 Knots [11% of the total individuals]). For the majority of birds, however, the large-scale weather systems present at the time of departure could have given assistance in a trans-Tasman flight. The rest could perhaps have staged in Northland before attempting to cross.

It is probable that birds from Farewell Spit attempt to fly directly to Australia. There are two main problems with making firm conclusions or predictions about these flights, both related to the use of flight range equations. The first is that travel speed (= flight + wind speed) has not been directly measured and may even vary between years. Flight range predictions varied by up to almost 800 km with a 10 km h⁻¹ change in flight speed and wind assistance (positive or negative) could easily cause larger variations. If, as suggested, birds are using large high-pressure systems to gain tailwind assistance, then flights to northern Australia or beyond would seem possible; there are records of New Zealand-banded or leg-flagged Knots in Irian Jaya (Pook 1992; Riegen & Davies 1993). Alternatively, if poor flying conditions are encountered, then landing in eastern Queensland may be all that is achievable (Knots from New Zealand have been recorded there also, Pook 1992; Riegen & Davies 1993).

The second problem is that flight range equations assume fat to be the only nutrient deposited before migration, which may not necessarily be so. Protein deposition can also greatly affect flight range estimates (Fig. 9). Knots from northern New Zealand deposit some protein before migrating (Battley & Piersma 1997), but our single small sample is unable to assess

this accurately. The indication, however, is that protein deposition is probably small relative to fat deposition.

Certainly, Knots in New Zealand do deposit a large amount of fat before migrating (Battley & Piersma 1997), so that most of the estimates of flight range (Fig. 9) suggest ranges well in excess of the minimum trans-Tasman flight, the majority allowing a successful flight to northern Australia or beyond. It may be that such apparent 'overloading' is a mechanism to allow for extended flight ranges when weather conditions are favourable, and to increase the chance of successful migration when they are not.

Potentially, Knots from New Zealand may be capable of very large flights. However, until better information is available on both flight/wind speeds and fat/protein levels, any conclusions must be tentative. Determining the probability of birds being able to achieve a given travel speed across the Tasman Sea (e.g. through meteorological records) would aid our interpretation of the first problem. The most direct insights would come from intense coordinated trans-Tasman ringing efforts in an attempt to get departure and arrival condition data (see Piersma & Jukema 1990 for an example of this approach with Godwits on the East Atlantic Flyway). The biggest handicap to this is that the Gulf of Carpentaria is largely inaccessible during the migration season. However, leg-flag sightings might indicate other sites in Queensland that could hold New Zealand birds.

In New Zealand there is no evidence for Arctic wader mortality being prominent over the non-breeding season and it is probable that migration may be a major cause of mortality for these birds. Given that waders are long-lived birds with high adult survival, periodic selection may be sufficient to drive migration patterns. A corollary of this is, of course, that when looking at the evolution and maintenance of migratory strategies, obvious strong selection pressures may be realised only intermittently.

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