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MIGRATORY DEPARTURES OF WADERS FROM NORTH-WESTERN AUSTRALIA: BEHAVIOUR, TIMING AND POSSIBLE MIGRATION ROUTES

INGRID TULP[1,2], STEVE McCHESNEY[3,4] & PETRA DE GOEIJ[1,2]

ABSTRACT Migratory activity of waders departing from north-western Australia in March-April 1991 was recorded by field observations and radar tracking. Field observations showed that the species concerned were mainly Bar-tailed Godwit *Limosa lapponica*, Grey Plover *Pluvialis squatarola* and Great Knot *Calidris tenuirostris*. Peak migration took place in the second week of April. Most flocks departed in the late afternoon, never at high tide. A strong correlation was found between the tidal cycle and the timing of departures. The majority of the flocks flew towards NNW. Given that the next stopover site of especially the larger sized waders is in east and south China (Barter & Wang 1990) this observed departure direction is more westerly than a course along the great circle route (0°). Wind patterns along two possible northward routes (a great circle and an island hopping route along the island-arc of South-east Asia) are analysed. In view of recoveries of waders ringed in Australia, especially the smaller waders (Mongolian Plover *Charadrius mongolus*, Large Sandplover *Charadrius leschenaultii*, Red-necked Stint *Calidris ruficollis*, Curlew Sandpiper *Calidris ferruginea*, Broad-billed Sandpiper *Limicola falcinellus*, Terek Sandpiper *Xenus cinereus*) may migrate via the island hopping route, while the larger ones (Grey Plover, Great Knot, Red Knot *Calidris canutus*, Bar-tailed Godwit, Whimbrel *Numenius phaeopus* and Eastern Curlew *Numenius madagascariensis*) take a direct, great circle flight to China. Considerable tail wind assistance can be gained during the northward trip, more so along the island arc than along the great circle. Flight range estimates indicate that the smaller waders cannot fly the 4500-5500 km nonstop to east and south China, while the larger species can, on the condition that they experience tail wind assistance.

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INTRODUCTION

Studies on the migration of waders travelling to and from their breeding grounds and wintering areas in the western Palearctic and Nearctic areas, have shown that waders are able to make journeys of up to 4500 km (Morrison 1984, Piersma & Jukema 1990, Zwarts *et al.* 1990). A trip of similar length performed by waders departing from north-western Australia and heading for their breeding grounds in eastern Siberia (Barter 1992a, Pook 1992) would bring them as far as South-east Asia. Ringing and recapture data of ringing groups operating along the Asian-Australasian Flyway have shown that the first likely stopover sites that large waders use on their way north are the vast intertidal areas in southern and eastern China (e.g. the Yangtze estuary near Shanghai, Barter & Wang 1990, Pook 1992, Barter 1992a; Fig. 1A). However, there have been some recov-

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eries of small wader species along the island arc of South-east Asia (Pook 1992). Radar studies in Hongkong and China confirm migratory passage: flocks moving southwest in the boreal autumn and north in the boreal spring (Myers & Apps 1973, Melville 1980, Ying & Zhou 1987). Small waders, leg-flagged in Victoria and at Eighty Mile Beach, Australia, are regularly sighted on north-bound migration in Hongkong (Minton 1993). In total 16 birds (Large Sandplover *Charadrius leschenaultii*, Red-necked Stint *Calidris ruficollis*, Curlew Sandpiper *Calidris ferruginea*, Broad-billed Sandpiper *Limicola falcinellus*), leg-flagged in north-western Australia were sighted in Hongkong on northward migration in 1993 (McChesney in press). Radar studies on Guam in the southern Pacific Ocean show migratory passage on both north- and south-bound migration

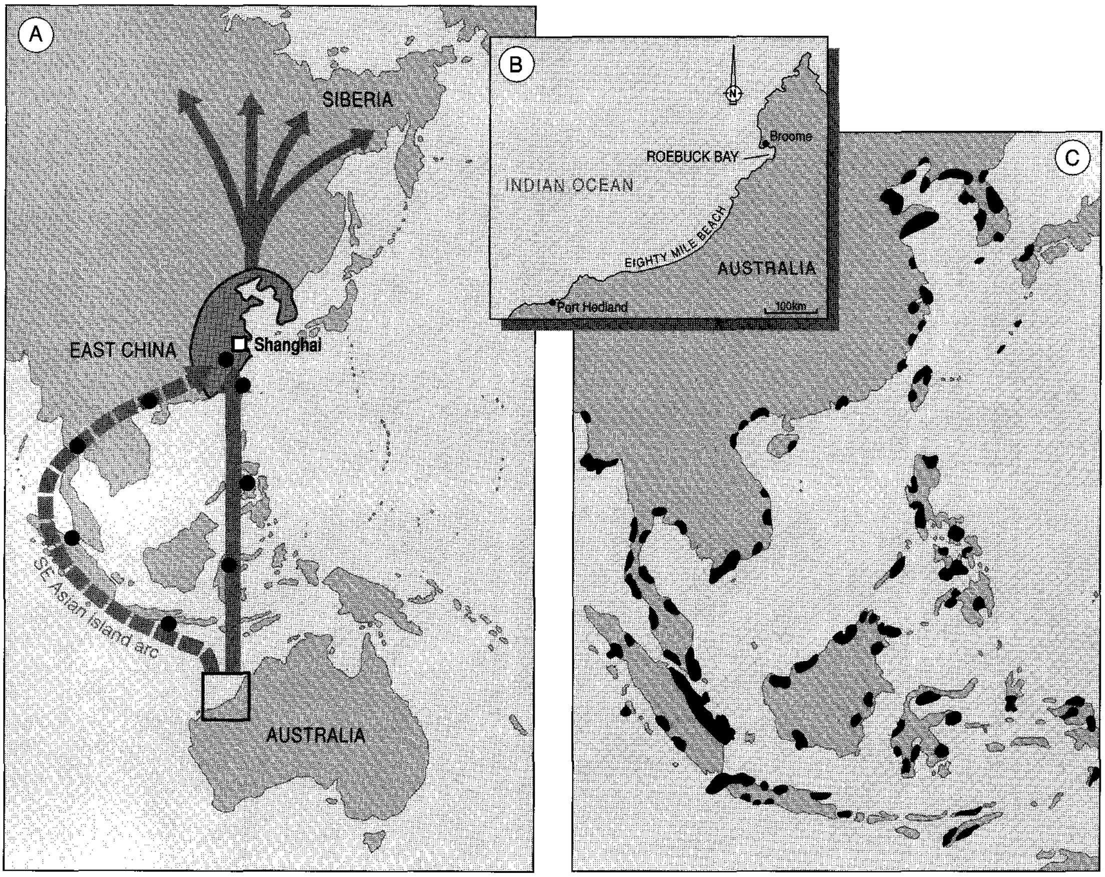

Fig. 1. Location of the observation site (B indicated by the square in the left panel) situated in the Asian-Australasian flyway. The shaded area indicates the known stopover area in China. The arrows (in A) indicate the two selected flyways. An island hopping route to east China is indicated by the dotted arrow while the solid arrow indicates a great circle route. Different read-out locations from the synoptic weather charts for the wind-analyses along the two flyways are indicated with dots. Panel C shows possible stopover areas in South-east Asia. For these selected wetlands information exists to determine that the site is suitable for migrating waders. Criteria for selection include: 1. salt or brackish water and/or, 2. soft-sediment beaches or mudflat and/or 3. recorded presence of waders (compiled from Scott 1989).

(Williams & Williams 1988, Williams & Ying 1990). Apparently there are many possible routes, leading along many possible stopover sites (Fig. 1C), that migrating waders may use.

The time elapsed between ringing in north-western Australia and recapture located approximately 5500 km due North was seven days for one Great Knot *Calidris tenuirostris*, and less than twelve days for two Bar-tailed Godwits *Limosa lapponica* and another Great Knot (Pook 1992). In March 1994 3 leg-flagged Great Knots, that were caught in north-western Australia were resighted only three days later in Hongkong 4500 km away (S. McChesney pers. obs.). These flights are too fast to include substantial extra fattening periods in South-east Asia. Furthermore the distance travelled is considerably longer than the distance their conspecifics travel along other flyways. Bar-tailed Godwits departing from the Banc d'Arguin in Mauritania only reach the Wadden Sea in one flight when their trip is helped by considerable tail wind assistance (Piersma & Jukema 1990). In this study we examine the question how waders migrating along the Asian-Australasian Flyway manage to fly up to 1000 km (20%) further than waders migrating from Mauritania to the Wadden Sea (Piersma 1987). Out of the large number of possible migratory pathways, we have arbitrarily selected two possible routes and analysed tail- or head-winds along them. In this paper we will call these routes the great circle route and the island-hopping route.

A successful flight may depend on the availability of flockmates, visibility, wind conditions and last minute feeding possibilities (Piersma *et al.* 1990). Therefore, the moment of take-off may be critical. We have examined these behavioural patterns at departure from north-western Australia. By comparing our results on departure timing, departure directions and calculated tail- or head-wind assistance with ringing recoveries along the Asian-Australasian Flyway we try to evaluate the possible routes the waders take northward from an energetic point of view.

METHODS

Field observations

All data were collected in 1991 on each day, except 19 April, during the migratory period 26 March to 30 April at Roebuck Bay, north-western Australia (18°01'S, 122°24'E; Fig. 1A, B: for a description of the study area see Tulp & de Goeij 1994). Systematic observations were carried out daily by 2-3 observers. Observation periods generally lasted from 16.00 h until darkness (18.30 h). Since observers were in the field for most of the day engaged in other fieldwork, additional observations were recorded whenever migratory activity was noted outside the systematic observation periods. Departing waders were followed with 10x40 and 8x40 binoculars and a 15x-45x telescope until the departing birds disappeared out of sight. Flocks that departed from the beach or mudflats, as well as flocks that passed by, were registered. Group size, species composition, behaviour and the occurrence of vocalizations were recorded. Compass bearings were taken at the instant that birds disappeared out of sight. When flocks did not pass overhead, but flew along side of us, we estimated the departure direction by taking the compass bearing when facing the same direction the birds were flying in, but parallel to their position (estimated error ± 5°).

For reasons of simplicity we will hereafter refer to two groups of waders: small and large waders. Small waders are defined as all species equal in size or smaller than Red Knot *Calidris canutus*: Mongolian Plover *Charadrius mongolus*, Large Sandplover, Red-necked Stint, Curlew Sandpiper, Broad-billed Sandpiper, Terek Sandpiper *Xenus cinereus*. Large waders include: Grey Plover *Pluvialis squatarola*, Great Knot, Red Knot, Bar-tailed Godwit, Whimbrel *Numenius phaeopus* and Eastern Curlew *Numenius madagascariensis*.

Radar tracking

From 26 to 31 March departing flocks were tracked between 17:00 h and 21:00 h, using the WF44 radar at the meteorological station in Broome (Fig. 1B). The radar has a wavelength of

10.4 cm and a beam width of 3.0° in both elevation and direction. Beam angle was varied between 0.5° and 2.5°, but 1.5° was used most often. Flock echos could be recognized as moving dots. We photographed echos with a polaroid camera mounted on a bracket fixed over the radar screen. Time-lapse photographs were taken at regular (15 minute) intervals to detect departing flocks of waders. Each photograph was taken by first opening the shutter for one minute, closing it for two minutes and opening it again for two minutes. The resulting photograph showed a dot, then a space, followed by a longer white dash, for each departing flock. Only clear dot-dash patterns were used in the analysis.

The trace length of the time-lapse echo image was measured to the nearest 0.1 mm from the center of the dot to the point in the leading edge of the dash image, one radius length of the dot inward (the images range in length between 1.0 mm and 4.0 mm). The trace length of the echo image represents the ground distance covered by the flock during the time the camera shutter was open. Hence ground speed was determined directly from the photograph.

From the directions of the dashes, the direction in which the flocks track can be determined. The distance from the radar to the flock and the angle of the radar disk provided an estimate of the maximum possible flight altitude of the flock.

Wind analysis

Local wind data were obtained from the meteorological station at Broome. The tail wind component effecting migrating waders along the two flight paths (great circle and island hopping paths) was calculated using two other data sets. Both sets include wind-speed and -directions at three different altitudes (1500 m, 3100 m, 5800 m). The first wind data are from monthly mean upper-level charts given by Chin & Lai (1974). They determined monthly average wind at stations, then drew flowlines illustrating the mean wind directions. For most stations, monthly mean wind data are from records through five years or more in the period 1965-1974. Chin & Lai (1974) cite Ramage (1959) and Wiederanders (1961) who 'have shown that 4-year averages very closely approximate to mean values for longer periods for stations over the Pacific'. The second wind data set comprises synoptic-scale constant pressure tropical strip charts available from National Oceanic and Atmospheric Administration (North Carolina USA). For this data set, we calculated tail- or head-wind components along the two routes for 21 departure days between 26 March and 15 April 1991. During this period 91% of the flocks and 97% of the individual birds departed from Roebuck Bay.

Tail- or headwind components were determined according to the methods described by Piersma & van de Sant (1992). They constructed travel schemes assuming that the birds started at 18.00 h and travelled with a constant ground speed of 65 km h^{-1}. Wind conditions along the possible flyways were read out at 8 locations indicated in figure 1A. The first wind measurement was read at 0.00 h, 6 hours after the birds had left Broome. Each subsequent measure was taken at 0.00 h of the following day. Wind vectors were calculated according to the formulae given by Piersma & van de Sant (1992). Calculated wind vectors were averaged over the migration period for three different levels (1500, 3100 & 5800 m), and for the optimal height, which is the level where the strongest tail winds prevail per read-out location. The use of this optimal track assumes that birds can sample winds in a vertical direction and then choose the optimal level at which to fly (Alerstam 1990).

Tidal data

Tidal data were obtained from tide tables determined by the port authority at the Broome jetty. The jetty is located approximately 15 km WSW from the migration observation points. Because of the extreme tidal range in Roebuck Bay (9 m at spring tide), vast intertidal mudflats are exposed at low tide. At the observation point, far into the bay, the tidal change was therefore earlier noticeable than at the Broome jetty.

Statistics and calculations

Statistical analyses were performed in Systat 5.0 (Wilkinson 1990) and in Statxact (Mehta & Patel 1992). Circular statistics were carried out according to Batschelet (1981).

To express mean flock sizes two different calculation methods were used: the $mean_1$ value represents the mean flock size from the observer's point of view and the $mean_2$ value is the mean flock size as experienced by the average bird. The former is calculated as $\Sigma x/n$ (x= flock size, n = number of flocks). The reasoning to arrive at the $mean_2$ value is as follows: There are x birds in the flock that all experience a flock of x birds. So the flock size as experienced by the average bird can be calculated as: $\Sigma x^2/\Sigma x$.

RESULTS

Migratory behaviour

When a flock of birds was about to leave,

Table 1. Numbers and flock sizes of departing and recruiting waders. For the explanation of the two different mean flock sizes see methods.

species	*n* flocks	*n* birds	($mean_1$) flock size	($mean_2$) flock size	range
Departures:					
Large Sandplover *Charadrius leschenaultii*	2	30	15 (7)	17 (8)	10-20
Grey Plover *Pluvialis squatarola*	11	476	43 (61)	116 (98)	10-210
Great Knot *Calidris tenuirostris*	10	795	88 (37)	96 (48)	30-135
Red Knot *Calidris canutus*	3	105	35 (33)	55 (41)	5-70
Bar-tailed Godwit *Limosa lapponica*	84	7896	94 (116)	235 (139)	14-700
Whimbrel *Numenius phaeopus*	6	190	32 (39)	72 (59)	10-110
Eastern Curlew *Numenius madagascariensis*	3	39	13 (6)	15 (7)	6-17
Grey-tailed Tattler *Heteroscelus brevipes*	1	30	30 (0)	30 (0)	
small waders	4	250	63 (42)	84 (49)	20-120
mixed waders[1]	3	536	179 (133)	245 (156)	36-300
Recruiting flights:					
Large Sand Plover	2	34	12 (3)	17 (3)	15-19
Grey Plover	3	68	17 (11)	22 (12)	8-30
Great Knot	5	820	168 (48)	177 (52)	120-150
Bar-tailed Godwit	25	1385	55 (43)	87 (53)	8-200
Eastern Curlew	1	15	15 (0)	15 (0)	
mixed waders[2]	1	100	100 (0)	100 (0)	

[1]Refers to flocks consisting of 300 Great Knots/Bar-tailed Godwits, 200 Great Knots/Red Knots and 36 Grey Plovers/Eastern Curlews.
[2]Refers to a flock consisting of 100 Grey Plovers/Bar-tailed Godwits.

flock members tended to vocalize loudly. In most cases the birds that were ready to leave had already gathered on the mudflats and were alternatingly sitting in a group on the mudflats and making restless flights in circles. During both these behaviours they vocalized. After this period of alternating bouts of flying and sitting in groups, which varied in duration from a few minutes to half an hour, a group would fly up vocalizing loudly, form a bunch or cluster that kept climbing and later turn into a v-formation or echelon (for description of the flock types see Heppner 1974, Piersma *et al.* 1990). Besides the flocks which we actually saw departing from the bay, we also recorded flocks that were already aloft and still ascending when flying over Roebuck Bay. Sometimes flights which looked like departures were aborted when the birds suddenly turned around and re-alighted on the mudflats. These flights may have a function in the recruitment of flock mates (see Piersma *et al.* 1990) and so we will call them 'recruiting flights'.

Flock size and composition

The departures of waders as recorded by field observations are summarized in Table 1. In total 10,347 departing birds (127 flocks) were recorded, and 2,412 birds (37 flocks) were engaged in recruiting flights. The majority of departing flocks consisted of only one species. Only 3 mixed-species flocks were recorded. Departing Bar-tailed Godwits dominated both flock and bird numbers. On average Bar-tailed Godwits also left in the largest flocks (but the value is considerably skewed by two flocks of 500 and 700 individuals, both leaving on the same day). Red Knots were

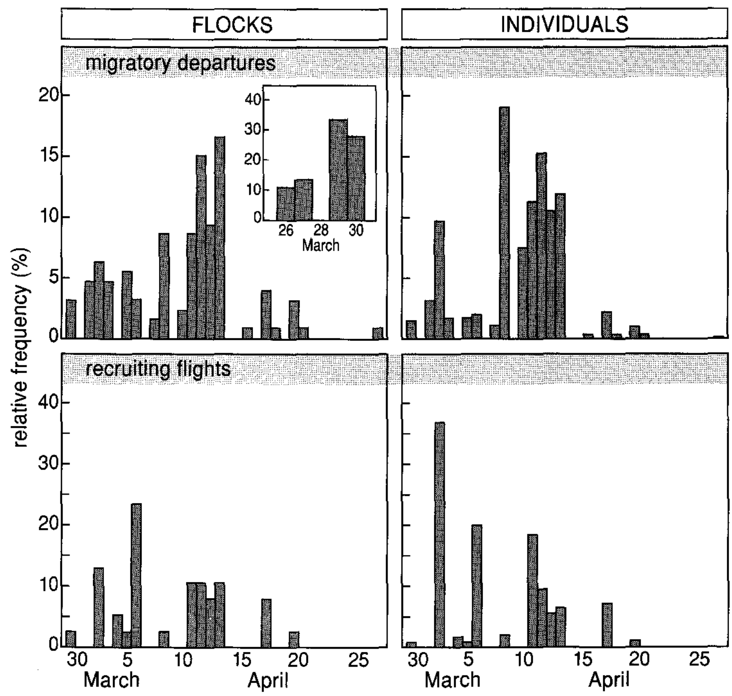

Fig. 2. Seasonal timing of migratory departures, based on visual observations. The upper panels show the frequency distribution of migratory departures of flocks (left) and individual birds (right). Frequency distributions of recruiting flights are given in the lower two panels for flocks (left) and individual birds (right). Data from radar tracking are presented in the inset figure in the upper left panel. Only in the first week of the period in which visual observations from the beach were carried out, radar recordings were made. Note the difference in scales of upper, lower panels and inset figure. Total sums of recordings are given in Table 1.

present in much larger numbers than the departure observations suggest, but the 2000 individuals present probably left the area on 19 April, when no observations were carried out.

The mean flock size as experienced by the average bird (mean$_2$ in Table 1) is larger than the arithmetic mean. The latter is the mean as experienced by the observers. This was also noted by Piersma *et al.* (1990) in waders that departed from the Banc d'Arguin. Flock sizes sometimes changed while birds were already in the air. The values given here all represent flock sizes as recorded when birds disappeared from sight. Recruiting flights were most often recorded in Bar-tailed Godwits (Table 1). In some cases flocks that were first recorded as recruiting flights later departed.

Seasonal timing

The first departing flocks were observed during the last week of March (Fig. 2). Peak migration took place during the second week of April. The greatest number of individuals left around 7 April. At the flock level, the biggest exodus took place around 12 April. Recruiting flights were timed simultanuously with the departures. During the six days of radar observations, peak migration took place on 29 March (31 flocks).

Great Knots departed earlier in the season than Bar-tailed Godwits (Fig. 3). The few small waders (in groups 'other' in figure 3) that we saw depart did not show a seasonal peak. Comparison with the numbers of waders present in Roebuck Bay (see Tulp & de Goeij 1994) shows that in early April the majority of the Great Knots and Bar-tailed Godwits had already left the area (940 and 450 left behind respectively, from the 3600 and 2000 present before the migration period). Since we recorded far more birds leaving than were originally present, the Bar-tailed Godwits that departed from the second week of April onwards were probably passing through and initiated their migration flights at other sites.

The peak in recruiting flights was timed slightly earlier than that of the departures (Fig. 3).

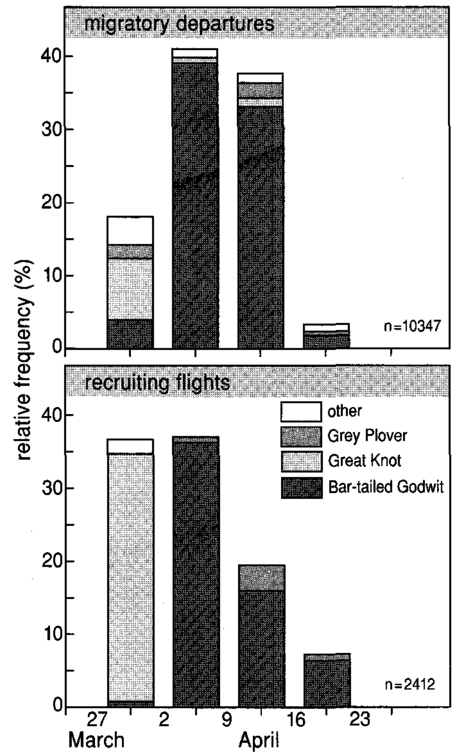

Fig. 3. Seasonal timing of migratory departures and recruiting flights per wader species. The category 'oher' consists of Large Sandplover, Red Knot, Whimbrel, Eastern Curlew, Grey-tailed Tattler and groups of small waders (see Table 1).

Diurnal and tidal timing

Highest intensity of departures and recruiting flights during daylight (Fig. 4) occurred in the 2-3 hours before sunset at 18.00 h (peak at 17.00 h). Five of the 127 flocks left early in the afternoon or even in the morning. Migratory departures occurred most often at rising tides (Fig. 5). No migratory departures or recruiting flights were recorded during high tide (Fig. 5). A smaller part of the departures took place at falling tide. The same pattern was found for recruiting flights. Recruiting flight intensity, analysed at flock level, shows a slightly different pattern, probably due to variation in flock size.

One complicating factor in clarifying the effect of either the tidal cycle or time of day as pos-

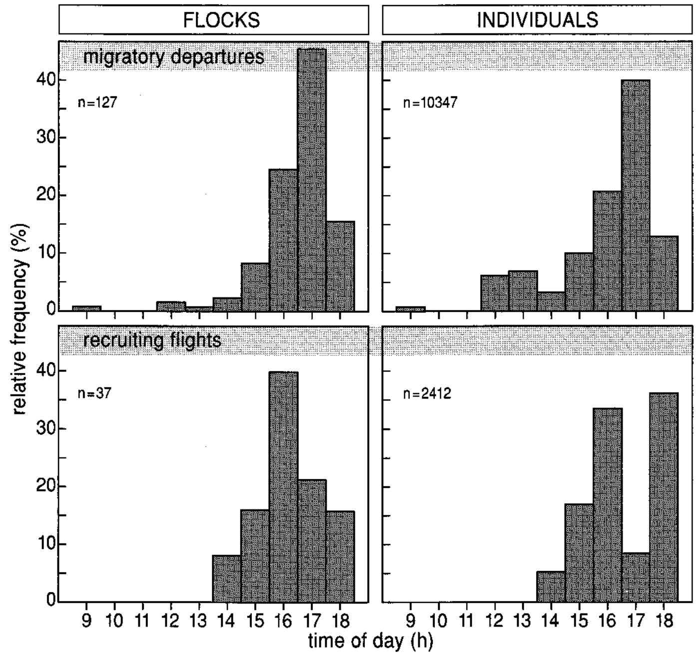

Fig. 4. Diurnal timing of migratory departures (upper panels) and recruiting flights (lower panels) on the basis of flocks (left panels) and individual birds (right panels). (Data from visual observations).

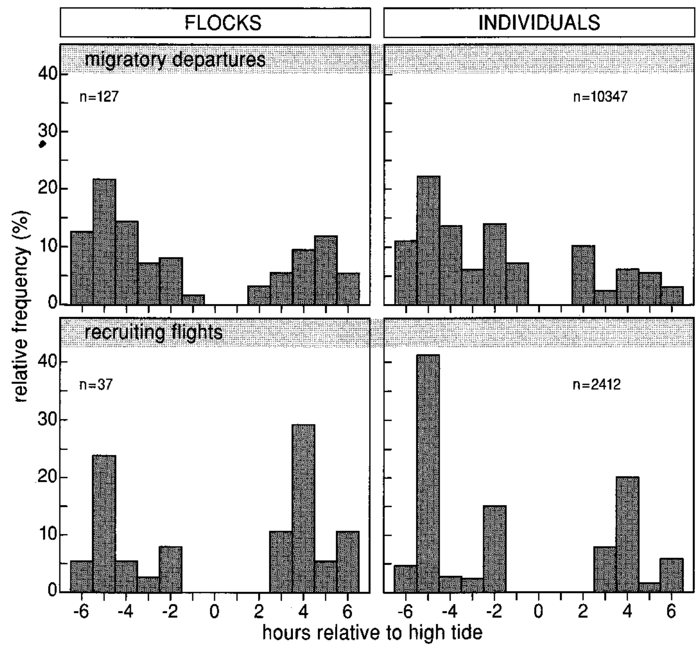

Fig. 5. Tidal timing of migratory departures (upper panels) and recruiting flights (lower panels) on the basis of flocks (left) and individual birds (right).

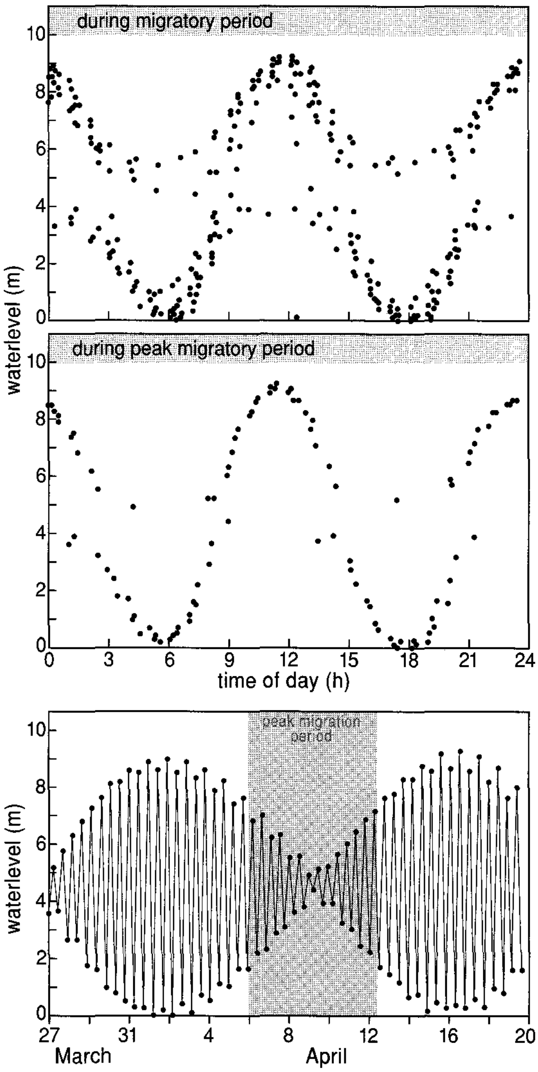

Fig. 6. Tidal variation in the complete study period (1 March-15 May, upper panel) and during the migration period (26 March-20 April, middle panel). The lowest panel illustrates the tidal range during the migration period (26 March-20 April). The shaded area indicates the peak migration period.

sible triggers is the aberrant course of the tidal cycle. The timing of the tide shifted steadily each day but at neap tides the tidal cycle shifted a few hours, which resulted in a roughly coinciding diurnal and tidal cycle. This means that high tides most often occur in the middle of the day and low tides therefore in the late afternoon (Fig. 6). This is the case during most of the whole lunar cycle, apart from the tides around neap tide. Strikingly, the few cases in which waders departed at times other than in late afternoon or in the evening, took place when the tide rose after sunset. On 17 April a flock of 80 Bar-tailed Godwit left at 9.20 h. On that day it was high tide at 11.52 h, low tide at 18.30 h, and the tidal range reached its maximum of 9 m. In spite of this, other flocks (of 25, 25 and 50 Bar-tailed Godwits and a flock of 20 small waders) left in the afternoon. Three recruiting flights of 65, 60 and 30 Bar-tailed Godwits also took place. The other occasion at which waders left early also took place during spring tide when the biggest flocks recorded during the study (500 and 700 Bar-tailed Godwits, 120 small waders) left at 12.00 h and 13.00 h respectively, just after high tide. None of these big flocks was observed taking off from our study area, so these might have been birds that had started off from an area southwest of Roebuck Bay.

Seen against the background of the tidal cycle, the peak migration took place around a neap tide period (Fig. 6, lowest panel). This of course might be coincidence and since the timing of neap tides differs between years it calls for a comparison of migratory timing between years.

Directions

95 flocks (of a total of 98) departed in directions between 280° and 20° (Fig. 7A,B). The mean directions of the departing and recruiting flights are given in Table 2. We failed to record the departure direction of 30 departing flocks. It was not useful to determine the flight direction of recruiting flights since these flocks often did not have a certain heading but just circled around several times before descending again. In some cases (18 cases in Table 2) the flights had the appearance of a real departure, although in the end the birds turned around and landed again. Departure directions of the small sample of small waders that could be identified did not differ from those of large waders (Watson-Williams test for differ-

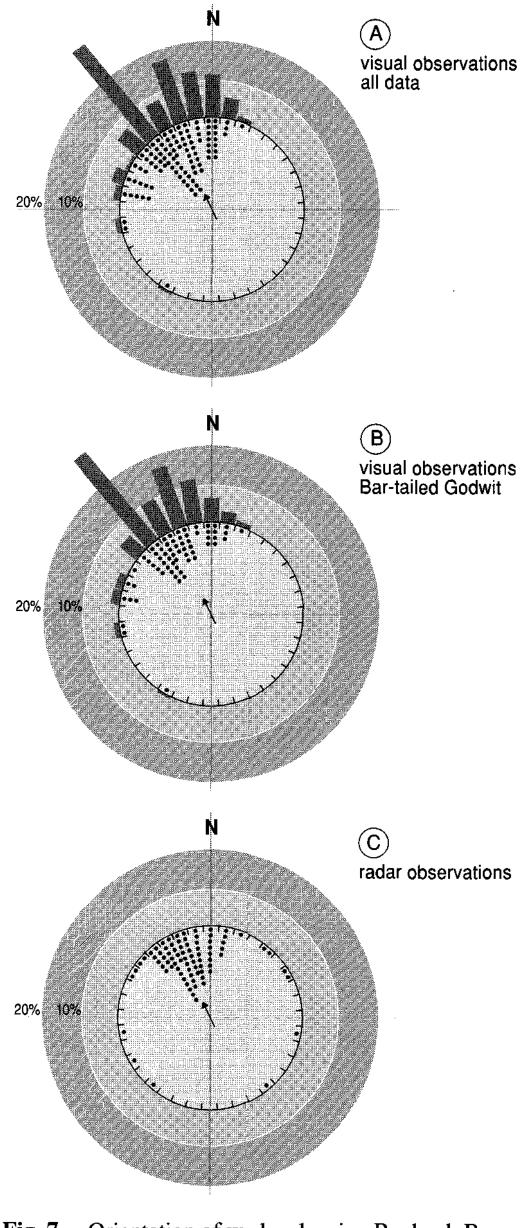

Fig. 7. Orientation of waders leaving Roebuck Bay recorded by visual observations (A and B). The upper graph shows the direction of orientation for all species (Table 2), data for Bar-tailed Godwit are summarized in graph B. Graph C presents data from radar analysis in the period 26-31 March. The data are divided in 10° sectors. Dots indicate flocks, bars show the frequency distribution of individuals in different sectors. The arrows in the middle of the the diagrams show the mean direction.

ences between mean directions, Batschelet 1981, $F_{1,100} = 0.10, p > 0.05$).

The mean direction based on radar observations (341°) shows a slightly more northerly direction during departure than those calculated on the basis of all field observations (329°), but the difference is not significant ($F_{1,180} = 0.97$, $p > 0.05$). For the days when both visual and radar observations were collected, we found no significant difference in mean departure directions ($F_{1,98} = 3.46$, $p > 0.05$) as recorded visually and by radar. The direction of the heading of the flocks does not show a change with distance from the radar.

Ground speed and altitude

Groundspeed of departing flocks ranged between 21.7 and 86.7 km h^{-1} (mean 47.0, SD = 14.7, n = 54). These values are low compared with values reported for a single evening of peak migration (16 April 1985) at the same site (range 51-91 km h^{-1}, mean = 78 km h^{-1}, Lane & Jessop 1985). The difference in groundspeed may be in part due to different species composition of flocks between the two years, as well as different wind intensities. Airspeed varied between 13.9 and 65.0 km h^{-1} (mean= 42.4 km h^{-1}, SD = 12.5, n = 54).

Average maximum altitude at which flocks were detected by radar was 804 m (SD = 204 m, range = 505-1600 m) but at the stage pictures were taken, flocks were probably still ascending (the range of the radar was only 56 km). We have probably not constrained the height to which waders climb on leaving Broome because of the low beam angle normally used (1.5°) to detect departing flocks and the short distance at which echos disappear (=20 km) prevented us from detecting waders flying above 980 m. Higher maximum altitudes were recorded when the radar angle was steeper.

Wind analysis for waders departing from Roebuck Bay

Since most of the flocks departed during the late afternoon (18.00 h) we used this as the depar-

Table 2. Mean orientation of flocks of departing and recruiting waders, recorded by field observations and radar photography (mean direction and length of vector and angular deviation are calculated according to Batschelet, 1981). An asterisk indicates the recruiting flocks. Mean values are only given for species with a sample size of 4 or more observations. Total number of large waders flocks is more than the sum of the separate species, since in this calculation all flocks (also with sample sizes less than 4) are incorporated. Sample sizes are smaller than given in Table 1 for most species, since compass bearings were not taken from all flocks. The small waders are unidentified. The category all (26-31 March) represents the flocks recorded in the same period as the radar observations were carried out.

species	direction mean vector (*deg*)	length mean vector (r)	angular deviation	number of flocks
Field observations:				
all	329	0.89	27	98
all (26-31 March)	327	0.93	21	22
Grey Plover	319	0.92	24	9
Great Knot	338	0.94	19	11
Bar-tailed Godwit	326	0.88	28	66
Whimbrel	337	0.85	32	4
small waders	334	0.96	17	4
total large waders	329	0.88	28	92
all*	334	0.95	18	8
Bar-tailed Godwit*	337	0.96	16	4
Radar:				
all	341	0.84	33	83

ture time in the analysis of the winds that the waders would encounter underway. The analysis of winds at Broome shows tail wind assistance at all levels on only about one third of the departure dates (Table 3). Birds that were leaving Roebuck Bay probably did not reach high altitudes soon after take off (altitudes recorded by radar did not exceed 1600 m, measured within a range of 20 km). If the departing waders had selected the altitudes with optimal winds (see Alerstam 1990) they would have encountered tail winds on nearly all of the departure days. As shown in other studies (Alerstam *et al.* 1990) departing waders climb steeply to high altitude just after take off, which is thought to enable them to sample winds on their way up and based on this sampling select the flight altitude at which the most favourable winds prevail.

On 29 March, when the peak migration in March was recorded by the radar tracking, there was tail wind assistance at the lower levels. No significant correlation was found between the occurrence of tail winds at any of the levels and the number of birds or flocks departing as recorded by field observations ($r = 0.32$, $r = 0.19$, $r = 0.04$, $r = 0.02$, $r = 0.15$, $r = 0.33$ for winds at the 50 m, 560 m, 1500 m, 3100 m, 5800 m altitudes and optimal altitude respectively). However wind analysis as presented here only involves winds in a restricted area at the start of the migratory journey. To see how wind patterns develop further along the route we have to analyse wind data on a bigger scale.

Table 3. Mean tail-or head wind components experienced by waders during the migratory period departing from Broome given for different altitudes. Tailwinds are indicated with a +, headwinds with a -. Standard deviations are given in brackets. Only data on which departures occurred are included. The number of birds that departed on each day is given in the last column.

date	wind vector (km h^{-1}) at: 50 m	560 m	1500 m	3100 m	5800 m	optimal height	*n* birds
27 March	-4.66	-7.47	+1.68	-23.27	-26.87	+1.68	160
29 March	+9.56	+13.58	+7.74	-13.32	-45.54	+13.58	325
30 March	+5.05	+3.58	+4.26	-6.45	-6.49	+5.05	1006
31 March	-0.42	+2.08	+2.07	-7.33	+8.55	+8.55	180
2 April	-1.46	+1.68	+7.61	+2.74	-0.85	+7.61	173
3 April	+0.86	-5.17	-9.01	+5.41	-22.02	+5.41	195
5 April	0.00	+3.36	-14.36	-11.19	-19.80	+3.36	100
6 April	-0.67	-3.60	-11.15	+5.06	-29.02	+5.06	1976
8 April	+1.79	-6.63	-2.14	-1.20	+7.25	+7.25	780
9 April	+4.80	+1.83	+3.43	-2.11	-2.30	+4.80	1175
10 April	+8.60	+1.65	-3.77	-10.21	-26.03	+8.60	1572
11 April	+1.60	-5.33	-3.73	-2.25	-11.05	+1.36	1090
12 April	+0.26	-18.00	-22.01	-2.56	+5.90	+5.90	1227
15 April	-3.82	-21.22	-54.17	-1.59	-13.15	-1.59	30
17 April	-1.46	-17.64	-10.41	+5.48	+13.45	+13.45	200
18 April	-2.94	-18.82	+1.32	-2.54	+18.56	+18.56	30
20 April	-0.85	-8.53	-4.95	-14.10	+6.15	+6.15	90
21 April	0.00	-3.53	-6.74	-6.49	+2.18	+2.18	30
average	0.81 (3.79)	-4.21 (9.05)	-5.94 (13.24)	-4.22 (7.53)	-10.07 (17.76)	6.17 (4.85)	

Wind analysis along two possible migratory routes

The read-out locations from the synoptic weather charts are given in figure 1A. Tables 4 (wind analysis on the basis of Chin & Lai 1974) and 5 (wind analysis on the basis of synoptic weather charts) illustrate that there is a substantially stronger tail wind vector along the island hopping route compared to the great circle route for both wind data sets. Table 4 illustrates the average case, while Table 5 represents the situation in 1991. Table 5 shows that 1991 was an average year with substantially stronger tail winds along the island hopping route. Winds along both flight paths get progressively stronger towards Shanghai, in some cases even too strong to remain on course. When birds are navigating along a route, the direction they are tracking is the vector sum of their heading and air speed and the wind direction and velocity. As wind velocity increases, birds flying at maximum airspeed must change their heading to remain on tract. At a certain wind force it is no longer possible for birds to compensate by changing their heading and they can not stay on course. In that case birds might try a different altitude where winds are gentler or land.

Flight ranges

One way to find out what route waders choose when starting off from north-western Australia is to examine how far they can fly with the fat stores that they are carrying. Although flight range estimates have been considered as highly variable and providing mostly underestimates (Davidson

Table 4. Mean tail- or head- wind components experienced by waders in April between Broome (northwestern Australia) and Shanghai (China) along the two possible flyways (based on wind charts by Chin & Lai 1974) Tailwinds are indicated with a +, headwinds with a -. Monthly mean wind data are from records through five years or more in the period 1965-1974.

altitude (m)	tail-or head wind vector ($km\ h^{-1}$) great circle route	island hopping route
1500	+2.82	+8.22
3100	-4.68	+10.53
5800	-2.36 *	+17.00 **
optimal height	+2.45	+17.34

* The last three stations on approach to Shanghai have winds too strong to remain on course: these stations are not included in the average mean tail- or head-wind component. The maximum airspeed of the birds is insufficient to compensate for winds this strong, so birds are unable to fly on course at this altitude.
** The last station on approach to Shanghai has winds too strong to remain on course: this station is not included in the average mean tail- or head-wind component.

Table 5. Average tail- or head- wind component ± *SD* (in brackets) along the two selected routes experienced by waders departing from Roebuck Bay between 26 March and 15 April 1991 and arriving in Shanghai 3.5 days later (great circle route) or 5.25 days later (island hopping route). Tail winds are indicated with a +, head winds with a -. Data are derived from synoptic weather charts.

altitude (m)	tail-or head wind vector ($km\ h^{-1}$) great circle route	island hopping route
1500	+0.55 (6.10)	+2.44 (8.16)
3100	+1.89 (5.77)	+9.46 (6.20)
5800	-4.06 (9.11)	+13.49 (6.20)
optimal height	+5.50 (5.01)	+15.64 (4.55)

1984, Piersma & Jukema 1990, Zwarts *et al.* 1990), we have tried to quantify the prospects of waders

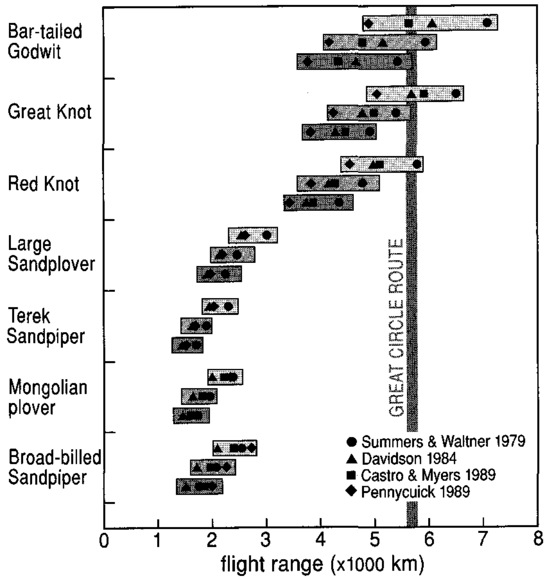

Fig. 8. Flight range estimates of 3 large wader species (Bar-tailed Godwit, Great Knot, Red Knot) and 4 small wader species (Large Sandplover, Terek Sandpiper *Xenus cinereus*, Mongolian Plover *Charadrius mongolus* and Broad-billed Sandpiper *Limicola falcinellus*) calculated according to 4 different authors. Species are ordered according to their size. The shaded bars indicate the variation in estimates at still air (heavily shaded bars), with 5.5 kmh^{-1} tail wind assistence (medium shaded bars) and with 15.6 kmh^{-1} tail wind assistence (lightly shaded bars). The vertical bar shows the distance to be flown to reach the East coast of Shanghai along a great circle route.

flying along two possible routes. Therefore we calculated flight ranges according to several authors. The empirical equation given by Summers & Waltner (1979) incorporates only departure and arrival body mass and considers the mass loss during a migratory flight as a result of fat depletion. They used a value of flight metabolism based on passerines and therefore they end up with very high flight range estimates for waders. To make their formula more applicable to waders, Davidson (1984) used flight metabolism values based on non-passerines. In addition Castro & Myers (1989) included wing length in their equation. The theoretical model of Pennycuick (1989) uses aerodynamic properties of the bird expressed in a lift/drag ratio. Figure 8 shows the estimated flight ranges for 3 large wader species (Bar-tailed Godwit, Great Knot, Red Knot) and 4 small wader species (Large Sand Plover, Terek Sandpiper, Mongolian Plover and Broad-billed Sandpiper) in still air and when assisted by tail winds at optimal altitudes along the two routes. Values used to calculate these flight ranges are given in Table 6.

Ringing recoveries

Evidence that the large waders tend to fly the distance to Shanghai non-stop is provided by an increasing number of recoveries there soon after ringing in north-western Australia (Table 7). One Great Knot was recaptured near Shanghai only 7 days after it was ringed in Broome; two Bar-tailed Godwits and another Great Knot were recaptured within 12 days (Pook 1992). In addition three leg-flagged Great Knots were resighted in Hongkong only three days after they were caught in north-western Australia (S. McChesney pers. obs). It is very unlikely that these birds could have flown the 7500 km along the island hopping route within this period, since they would require an additional stopover to refuel along the way. In several

Table 6. Departure and arrival body mass, wing length and wing span values for 3 large and 4 small wader species as used to calculate flight ranges according to the different references. References for body mass values are given in the last column. Wing spans were obtained from unpublished data from Piersma and if not available, calculated from the equation given below.

species	body mass (g) departure	arrival	wing length (mm)	wing span (mm)	reference
Great Knot	230	120	195	570	Barter & Wang (1990)
Red Knot	165	87	165	475	Barter & Wang (1990)
Bar-tailed Godwit	350	196	225	711 *	Barter & Wang (1990)
Large Sand Plover	110	76	144	429 **	Barter & Barter (1988)
Mongolian Plover	84	61	136	403 **	Barter (1992b)
Broad-billed Sandpiper	55	37	112	328 **	Fry (1989)
Terek Sandpiper	95	71	137	407 **	Fry (1990)

* Wingspans were calculated from the relation between wing length and wing span of European Bar-tailed Godwit subspecies (wingspan = 0.295·wing length+4.736, $R^2 = 0.52$).
** Wingspans were calculated from the equation including the species of which both wing length and wing span were known (wingspan = 3.162·wing length-26.566, $R^2 = 0.98$).

Table 7. Summary of recoveries of waders ringed at Eighty Mile Beach or Roebuck Bay in north-western Australia and recovered the same season (within a month) elsewhere (after Pook 1992).

species	recovery location	ringing date	date of recovery	direction (°)	time elapsed (days)	distance (km)
Great Knot	Shanghai China	31/3/88	25/4/88	0	25	5627
Great Knot	Shanghai China	27/3/90	3/4/90	359	7	5426
Great Knot	Shanghai China	27/3/90	8/4/90	359	12	5426
Red Knot	Shanghai China	3/4/88	3/5/88	0	30	5540
Bar-tailed Godwit	Shanghai China	4/4/90	15/4/90	1	11	5642
Bar-tailed Godwit	Shanghai China	4/4/90	16/4/90	0	12	5564

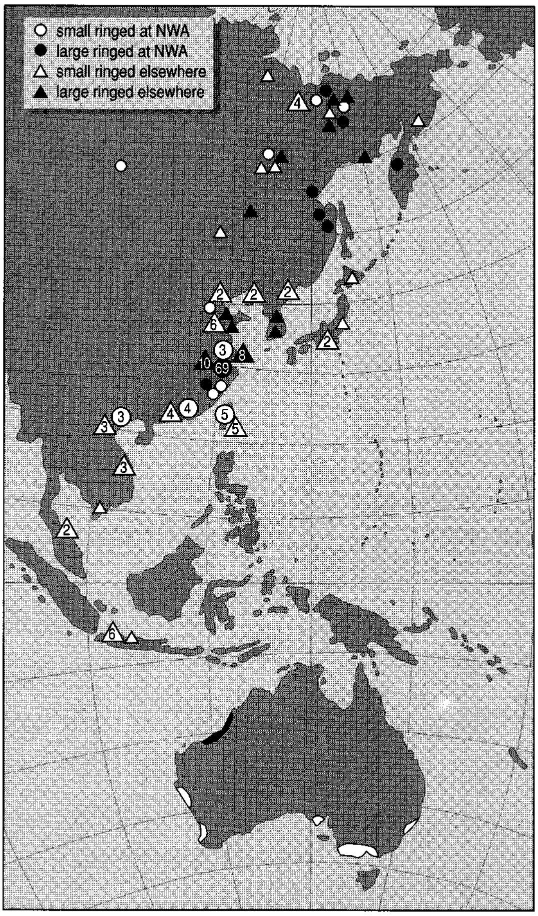

Fig. 9. Recoveries of small (open symbols) and large (closed symbol) waders ringed at north-western Australia (Roebuck Bay, Eighty Mile Beach and Port Hedland) (indicated by dots) and elsewhere in Australia (Victoria, New South Wales and south-western Australia) (indicated by triangles) based on Pook 1992. When more than one bird was recovered at a certain site, this is indicated by an enlarged symbol enclosing the number of recoveries. Catching areas in north-western Australia and other parts of Australia are indicated by black parts and white parts respectively.

studies is shown that long-distance migrants often need two or more weeks to refuel at stageing areas (Knots in Iceland and Norway: Gudmundsson *et al.* 1991, Strann 1992; Bar-tailed Godwits in the Wadden Sea: Piersma & Jukema 1990) Since the smaller waders can only fly 2000-3000 km with the fuel they carry (Fig. 8), they have to use wetlands in South-east Asia to refuel on their way north. If they do fly along the island hopping route they can take advantage of stronger tail winds compared to the great circle route.

Recoveries of waders ringed in Australia show that only small waders are recaptured along the island arc of South-east Asia (Fig. 9). These small waders were all ringed at areas in Australia other than north-western Australia. A study on the east coast of Sumatra showed that the area is used on northward migration (Silvius 1987). Two sightings of small waders leg-flagged in Victoria have been reported, one on Java, the other in Brunei. No sightings of small waders leg-flagged in north-western Australia have been reported (Minton 1993). Small waders leg-flagged in both Victoria and north-western Australia showed up in Hongkong (McChesney 1994).

DISCUSSION

Timing of migration

Departures reported in this study occurred slightly later than reported in Lane & Jessop (1985), who carried out a similar study in the same period of the year in 1985 in the same area. They recorded most departures during the last week of March and the second week of April. Starks & Lane (1987) reported the last week of March and the first week of April as the main departure period for Bar-tailed Godwits and Great Knots.

Migratory departures occurred most often at rising tides (conforming to the findings described by Lank (1989) and Piersma *et al.* (1990)(Fig. 5)). In a number of studies (Richardson 1979, Lank 1989, Alerstam *et al.*1990, Piersma *et al.* 1990, Gudmundsson 1993) migratory departures were reported in the late afternoon. Alerstam *et al.* (1990) report that significant differences in diurnal timing between years were associated with between-year differences in the tidal cycle. In this case waders (Knots and Turnstones *Arenaria* *interpres*) in NW Iceland also departed in the late afternoon, but since they apparently preferred to depart during rising or high tide, the median departure time was associated with the temporal shift in the tidal cycle between years. A correlation between departures and the tidal cycle was reported by Lank (1989), who found that when departures of Semipalmated Sandpipers *Calidris pusilla* occurred early in the day, they were associated with rising tides, while departures prior to sunset occurred on falling or low tides.

Lank (1989) suggested that birds started to migrate when the foraging opportunity was relatively low. In the case of visually foraging waders, this occurs at both the high tide periods and during night. He reported that Semipalmated Sandpipers left after low tide, so that they could leave with a full stomach. On the other hand Swennen (1992) found that Knots never left 'with a full stomach', but only approximately 2 hours after they had stopped feeding.

In our study area only a small portion of the intertidal mudflat stayed exposed for nearly the complete tidal cycle during neap tides. So birds were able to forage almost all the time but only on a restricted area. The opportunity to forage for a few days without being restricted by the tide might be beneficial for waders that are about to leave. However, feeding opportunities for birds foraging on the restricted area that is exposed at neap tides might be lower due to depletion of prey, prey avoidance behaviour, or lower standing stock (Tulp & de Goeij 1994).

From these previous studies the influence of both the day/night rhythm as well as the tidal cycle on the timing of migration become clear. Since in this study the tidal cycle and the day/night rhythm were correlated (high tides always falling around noon, except at neap tides) we cannot distinguish between the effects of each factor on migratory activity. In our study departures only took place during rising and falling tides. Apparently birds choose between either leaving after a good feeding period before the tide was high or waiting until after high tide.

When comparing figures 4, 5 and 6 there seems to be a discrepancy. Figure 4 clearly shows that peak departures occur in the late afternoon. According to figure 5 there is a peak in departures at both rising and falling tides. The discrepancy arises when comparing these two figures to figure 6, which describes that tides are only falling at peak departure time of day (17.00 h). Data presented in figure 6 were determined at the Broome jetty 15 km WSW of the observation site. Because of the geographical location of the bay the timing of the tidal cycle was slightly earlier at the observation site than at the jetty. The extreme tidal range in Roebuck Bay exposes a vast mudflat area at low tide. At the water's edge the tide changed some time before the tidal change reached the jetty and the effect of changing tides was more drastic due to the very gradually sloping shore than at the jetty, where the waterlevel was measured in the very deep water of the harbour. The onset of the rise of the tide will therefore be more and earlier noticeable on the mudflats than in the harbour.

One explanation for leaving at changing tides already put forward by Piersma *et al.* (1990), Gudmundsson & Lindström (1992) and Swennen (1992) is that the disturbance by changes in water level might put the birds in the air and through that elicit departure. Piersma *et al.* (1990) compared several studies on tidal timing of migration and showed that the correlation between tidal cycle and timing of departure becomes stronger with increasing tidal ranges. The situation of departures from Roebuck Bay, an area characterized by a tidal range of 9 m at maximum, fits perfectly well in this pattern (Fig.10). The 'tidal influence index' (see figure caption for explanation), calculated in order to obtain a value for the tidal effect on migratory departures, increases with increasing tidal range. This finding supports the idea that disturbance by moving water might trigger departures, since the tide in areas with a large tidal range will probably rise and fall at a higher speed than in areas with a smaller tidal range.

Departure directions

Lane & Jessop (1985) found that the main de-

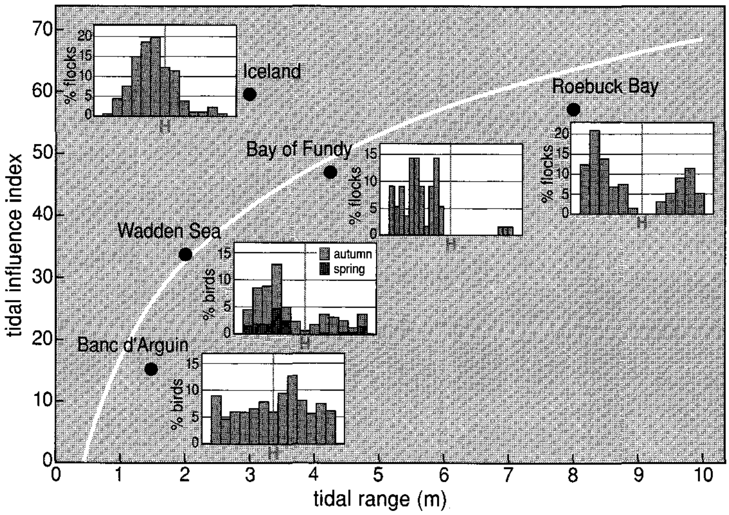

Fig. 10. Tidal influence index as a function of tidal range. Tidal influence index is calculated by summing the absolute differences between the observed frequency distribution and the expected frequency distribution if tide did not affect the timing of departure at all (so at any tidal stage the same amount of birds would depart). Because we were mainly interested in the reaction of the birds to the *moving* water, the frequencies before and after high tide have been added (so the value for -6 h was added to +6 h, -5 h to +5 h etc.). Inset figure s show the timing of migratory departures in relation to the tidal cycle in different areas (with H representing high tide). The line is drawn by hand. Data are derived from Piersma *et al.* 1990 (Mauritania, Wadden Sea), Alerstam *et al.* 1990 (Iceland), Lank 1989 (Bay of Fundy), Roebuck Bay (this study, see also figure 5).

parture direction was between 339° and 344°, values very similar to our radar measurements. The departure directions as recorded both by radar and by field observations were oriented in a more westerly direction than a course along the great circle route (0°) would require. However, there are many directions in which waders could depart if they are heading for the island hopping route. Gudmundsson (1993) also found a difference between departure direction as recorded from field observations and by radar. The difference we found can probably be explained by the fact that the detection range of the radar is much larger than that of field observations. By the time the radar lost track of the flocks, they had already flown out of the bay, the entrance of which was oriented in a northwesterly direction. In the case of field observations, flocks could only be observed while they were still in the bay. It is possible that the waders first flew out of Roebuck Bay and only then adjusted their track towards the desired direction, as also noted by Strann (1992). He reports that waders in northern Norway first flew out of a fjord before finally heading towards presumed breeding grounds.

Approximately 25 out of the total of 98 departing flocks observed from the beach and 23 out of 83 departing flocks as recorded by radar headed due north. The majority of flocks headed in a northwesterly direction. It would be very speculative to conclude on the basis of the recorded departure directions what route they choose. The variation in departure directions allows a variety of migration directions and does not exclude one of the described routes, nor any intermediate alternative.

Methods for wind analyses

One disadvantage of using monthly mean wind vectors (e.g. Chin & Lai 1974) to evaluate tail- or head-wind components is that waders such as Great Knot and Bar-tailed Godwit can fly the distance in less than 7 days (Barter & Wang 1991). Furthermore these monthly mean charts are not sensitive to weather conditions that may be very severe but not long-lasting (e.g. tropical cyclones). Moreover the variation in wind patterns is not reported on the monthly mean charts and therefore the predictability of the tail- or head wind vector can not be estimated. The monthly mean wind analysis may be more appropriate for smaller wader species like Curlew Sandpiper and Red-necked Stint, because banding recoveries seem to indicate that they utilize more stopovers and take a longer time migrating (Fig. 9). Since the method of Piersma & van de Sant (1992) is more sensitive to weather events of brief duration than the monthly mean averages, this method is more appropriate for the long distance jumps made by the larger waders.

Flight paths in terms of time and energy

Flight ranges Flight range estimates that have been calculated to date for waders departing from north-western Australia (Barter & Barter 1988, Barter & Wang 1990, Thomas 1987) are based on much higher air speed values than in this study. We used the species-specific optimal flight speeds, calculated with Pennycuick's model (Pennycuick 1989). None of the predictive equations takes into account the energetic benefit the birds gain of flying in flocks (Heppner 1974). On the other hand all predictive equations assume the stores used during migration consist of 100% fat while birds also use protein on migration (Piersma & Jukema 1990, Lindström & Piersma 1993). The estimates according to Summers & Waltner (1979), especially in the large sized waders, are the highest. The relative differences between the estimates are more pronounced in the larger species.

Although flight range estimates as calculated according to the different equations vary greatly, it is clear that the small waders will never be able to fly the 4500-5500 km required to reach the wetlands near Hongkong or even Shanghai on a non-stop flight. The values predicted by Summers & Waltner (1979), Davidson (1984) and Castro & Myers (1989) would allow the larger species to reach there in one go only if the birds encounter a considerable tail wind. Pennycuick's theoretical model predicts flight ranges that would be a little short to do this, but taking the energetic benefit of flying in flocks into account it might be possible for them to reach this area.

Ringing recoveries Why are there no recoveries of small waders along the island arc of South-east Asia which were ringed in north-western Australia? First of all, little is known about the intensities of catching activity at the various spots along the routes or the probabilities of each bird species to get caught. Undoubtedly waders are being caught on the islands between Australia and China for human consumption, but rings are not being reported (pers comm. D. Melville). If we had reliable recovery information from these areas we could calculate the expected number of recoveries along the island arc. Since it is nearly impossible to estimate the probability of different species being caught as well as the varying levels of catching effort, we assume for now these factors are equal for all bird species in all areas. Table 8 summarizes the total number of birds ringed and recaptured at the various places (based on Pook 1992). On the basis of the assumptions mentioned above the numbers of small waders controlled (9 and 45 for small waders ringed at north-western Australia and Victoria respectively) does not differ from the expected numbers on the basis of ringing totals from north-western Australia and Victoria (South-east Australia) (p = 0.40, since sample sizes were small and the likelihood-ratio test statistic is only asymptotically chi-squared distributed, the p-values are calculated with the aid of the computer program Statxact). When comparing recoveries of small waders (Red-necked Stint, Curlew Sandpiper, Sharp-tailed Sandpiper *Calidris acuminata*) that have either been ringed in north-western Australia or in Victoria, expected numbers of recoveries along the island arc (in this case defined as ranging from

Vietnam southwards) or along the Chinese coast do not differ significantly from actual numbers of recoveries ($p = 0.07$). Since small waders (in this case including the most commonly ringed species: Mongolian Plover, Large Sandplover, Ruddy Turnstone, Terek Sandpiper, Sharp-tailed Sandpiper, Red-necked Stint, Curlew Sandpiper, and Broad-billed Sandpiper) are largely overrepresented in the total numbers of waders ringed (79,160 out of 85,619 in Victoria and 18,857 out of 32,882 in north-western Australia) we also examined the number of recoveries of large and small waders along the island arc and along the Chinese coast. On the basis of the total number of ringed waders, there was a significant difference between the number of recoveries of both small and large waders and the expected number of recoveries ($p < 0.001$). This means that on the basis of numbers ringed, less than expected small waders and more than expected large waders were recovered along the Chinese coast, while the situation was reversed in the case of the island arc. Regarding the very high number of recoveries near Shanghai and relatively low number of recoveries in South-east Asia the presumption that catching effort differs between the locations seems justified.

Table 8. Summary of total waders ringed and recovered at the various places. The classifications of waders as either 'large ' or 'small' are given in the text. NWA represents north-western Australia, VIC represents Victoria.

type wader	small		large	
ringing location	NWA	VIC	NWA	VIC
total ringed	18 857	79 160	14 025	5 459
recovered along island arc	0	13	0	0
recovered along Chinese coast	9	32	70	9

Although small waders were present in quite large numbers during the study period, very few flocks were observed taking off. Zwarts & Piersma (1990), who noticed a similar effect in Mauritania, suggested that small waders might easily be overlooked or that they departed in different directions. If small waders departing from north-western Australia head for the islands of South-east Asia, the first flight to make is probably relatively short (Fig. 1). Therefore the importance of impressive departure ceremonies to recruit flock mates and determine the right timing of departure may be less than for larger waders that are leaving for a 5500 km non-stop flight.

As stated above there are many uncertainties about the trapping methods, catching intensities and recovery rates. We doubt that with the catching methods used different species have similar chances of being caught, for instance the number of recovered Great Knots is very high compared to other species (Pook 1992). There is an urgent need to increase the knowledge of bird movements through the Phillipines, Sulawesi, and Borneo and surrounding islands as this information is crucial to the understanding of the Asian-Australasian flyway.

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SAMENVATTING

Door middel van veldwaarnemingen en radar fotografie is de wegtrek van steltlopers vanuit noordwest Australië bestudeerd. De betreffende soorten waren voornamelijk: Rosse Grutto *Limosa lapponica*, Zilverplevier *Pluvialis squatarola* en Grote Kanoet *Calidris tenuirostris*.

De piek in de wegtrek trad op gedurende de tweede week van april. De meeste groepen vertrokken laat in de namiddag, ze vertrokken nooit tijdens hoog water. Een sterke correlatie is gevonden tussen de getijcyclus en de timing van vertrek. De meerderheid van de groepen vertrok in noordnoordwestelijke richting.Gegeven dat de volgende pleisterplaats van vooral de grotere soorten in oost en zuid China is (Barter & Wang 1990), is dit westelijker dan een grootcirkel route.

Wind patronen langs twee mogelijke routes noordwaards (een grootcirkel en een route langs de eilandenboog van zuidoost Azië) zijn geanalyseerd. Met het oog op terugvangsten van steltlopers, geringd in Australië, zouden vooral de kleinere soorten (Mongoolse plevier *Charadrius mongolus*, Woestijnplevier *Charadrius leschenaultii*, Roodkeelstrandloper *Calidris ruficollis*, Krombekstrandloper *Calidris ferruginea*, Breedbekstrandloper *Limicola falcinellus*, Terek Ruiter *Xenus cinereus*) een route langs de eilanden van zuidoost Azië kunnen nemen, terwijl van de grotere soorten (Zilverplevier, Grote Kanoet, Kanoet *Calidris canutus*, Rosse Grutto, Regenwulp *Numenius phaeopus* en (oosterse) Wulp *Numenius madagascariensis*) een meer rechtstreekse grootcirkel route naar China wordt verondersteld.

De steltlopers kunnen een aanzienlijke rugwind ondervinden op beide onderzochte routes, maar veruit het voordeligst is de route langs de zuidoost-aziatische eilanden. Schattingen van het vliegbereik tonen aan dat de kleinere soorten de 4500-5500 km naar oost en zuid China niet non-stop kunnen vliegen, terwijl de grotere soorten dit alleen kunnen op voorwaarde dat ze rugwind ondervinden.