

# Day- and night-time movements of radiomarked Red Knots staging in the western Wadden Sea in July–August 1995

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Fourteen individually radio-marked Red Knots *Calidris canutus* staging in the western Wadden Sea in July–August 1995 often wandered considerable distances in the course of a single tidal cycle, which confirmed previous ideas based on movements of flocks observed. The birds continued this tidal feeding rhythm during nighttime darkness. There was a tendency for Red Knots to remain for shorter periods on the high-tide roost at night than during the day. Individual birds with body masses > 140 g when radio-marked (which may have been close to departure for West Africa), were less itinerant than light-weight individuals and were more likely to feed in an area close to the roost where relatively soft-shelled shorecrabs made up much of the diet. Such mass-related differences in foraging movements may be explained by migration-related physiological changes, different needs to track changes in local food stocks and to find suitable flock-mates to take-off with and body mass related predation and starvation risks and flight costs.

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## INTRODUCTION

Red Knots *Calidris canutus* breed in the High Arctic and spend the non-breeding season on intertidal mudflats in temperate and tropical zones, feeding mainly on buried bivalve prey. In the western Wadden Sea, The Netherlands, where this study took place, two subspecies occur. Members of the *islandica* subspecies, breeding in Greenland and Northeast Canada, stay from August to April, and use the area as their moulting and wintering site (Davidson & Wilson 1992). The *canutus* subspecies, breeding in north-central Siberia, only stops over in July–August and in May, on the way to and from their West-African winter quarters (Piersma *et al.* 1992).

In the western Wadden Sea both populations make intensive use of the intertidal flats around the small uninhabited islands of Griend and Richel for feeding. The two islets, which are free of mammalian predators but not necessarily of avian predators, are used as roosting sites during high tide. In an earlier study, Piersma *et al.* (1993a) provided evidence based on movements of flocks observed in the day-time that Red Knots may cover an area as large as 800 km<sup>2</sup> in a couple of tidal cycles in their search for food and safe roosting sites.

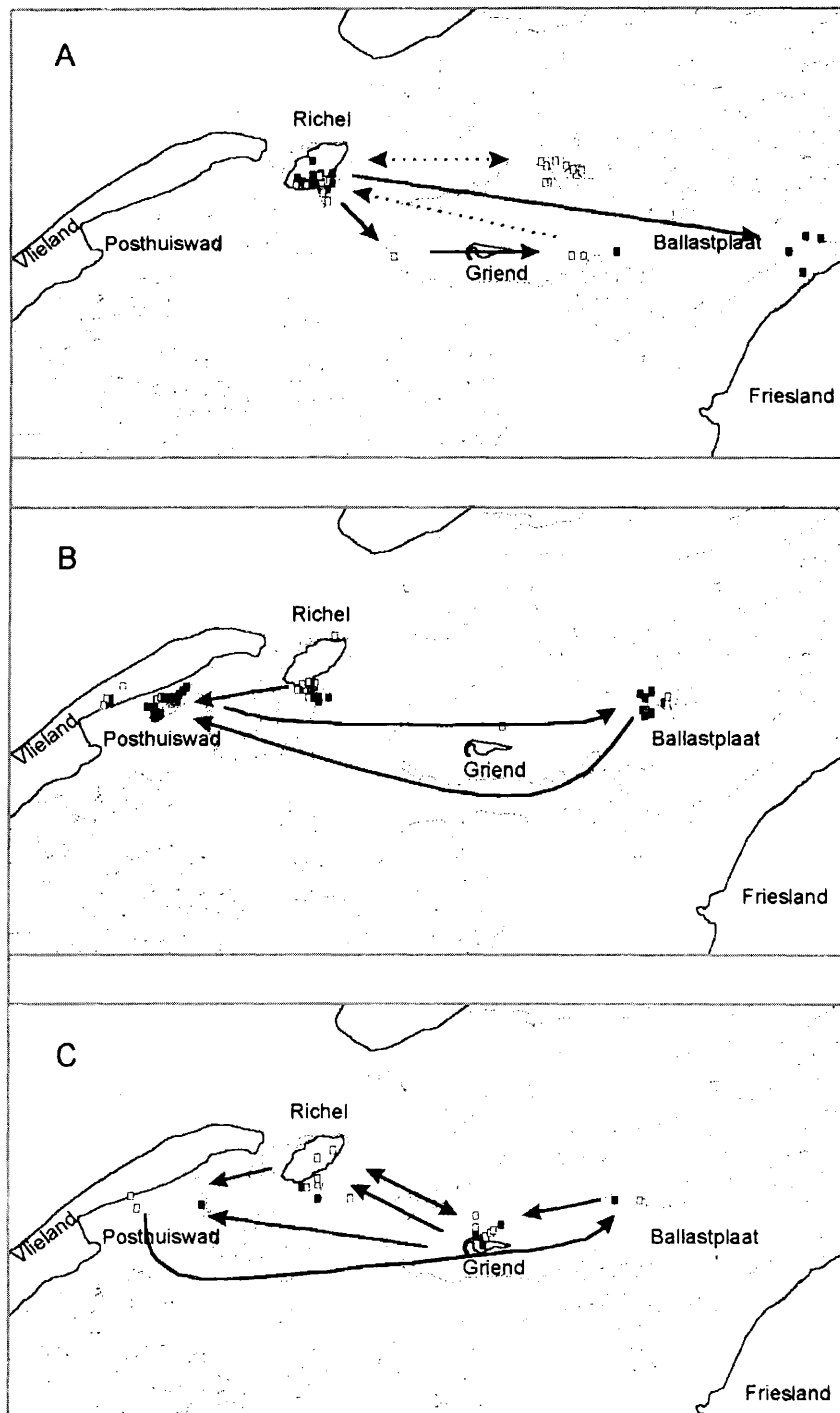
The large-scale movements described by Piersma *et al.* (1993a) were based on observations of flocks during daytime. Here we report on our first attempt to measure these patterns

at the individual level during day and during night. We aimed to test whether: (1) individual Red Knots staging in the western Wadden Sea in late summer/early autumn can be confirmed to cover a large area of intertidal flats during single low water periods, and (2) whether this ranging pattern is maintained at night. We have used radiotelemetry as a means to achieve this aim. For the benefit of readers, references on the use of radiotelemetry in studies of wader behaviour have been assembled in an Appendix.

## MATERIAL AND METHODS

At Richel, one of the most important wader roosts in the western Wadden Sea, we mistnetted 52 Red Knots in late July 1995. We glued radio-transmitters on the backs of 14 Red Knots, using superglue rather than epoxy (Raim 1978), but otherwise followed the instructions of Warnock & Warnock (1993). Based on the absence of primary moult, 10 of these Red Knots presumably belonged to the *canutus* subspecies breeding in Siberia. The other four birds belonged to the *islandica* subspecies, one being a one-year old bird in advanced wing moult that was likely to have spent the summer in the Wadden Sea, the rest being adult birds in wing moult (Table 1). All birds were molecularly sexed using small blood samples stored in 70% ethanol (Baker *et al.* 1999). The birds were weighed to the nearest gram on an electronic balance, their bill length, total head, and tarsus plus toe length measured to the nearest 0.1 millimetre with calipers, and wing





**Figure 1.** Examples of movements of individual Red Knots through the western Wadden Sea. Filled squares indicate positions during the night, open squares are positions in daytime. [A]. Movement pattern of female *canutus*-Knot (#212), 1–4 August. In the first night, between 000–3:55 h, the bird is roosting at Richel, whereafter she feeds south of Richel until 7 h. During the next low tide period she feeds west of Griend for a short time, before moving to the flats east of Griend in the evening. Next morning she is found northeast of Griend till noon. That late evening until the early morning she is found on the mudflats close to the Frisian coast. [B]. Almost the whole of 13 August was spent by the same female *canutus*-Knot #212 at and near Richel, before moving on to the flats near Vlieland during the night. During the subsequent daytime low tide period she was northeast of Griend, where she was recorded again at night until late morning. That evening she was found to pass westward south of Griend, probably flying from feeding grounds in the east. She roosted at Vlieland, whereafter she fed on Posthuiswad at night. [C]. This map shows the movements of female *islandica*-Knot (#249), over a period of almost 100 hours, 11–16 August. In the first night the bird is roosting at Griend, but flew to Richel (a distance of 9 km) in the early morning where she probably continued to roost. Then she started to feed at the flats around Richel. At noon that day, she was again recorded roosting at Richel. The next high tide she is roosting at Griend. That night she flew to Richel where she continued roosting, to be recorded feeding close to Richel the next low tide. About half a day later she is feeding south of Vlieland (7 km away), and at the end of that day she feeds east of Griend, implying another flight of 23 km. Next morning she is found there once more, whereafter she roosts at Griend in the afternoon (a distance of 7 km). That night she is recorded south of Vlieland again, presumably feeding (16 km). Over the period of observation this bird has flown a minimum of 80 km, or 20 km/day.



**Table 1.** Summary of biometrics, sex, age and subspecies of the 14 Red Knots radio-marked in late July 1995. All birds were caught at Richel, during night-time high tides. Radio frequency at the 173 MHz bandwidth is given. (c.y.=calendar year).

Radio frequency (kHz)	Capture date	Body mass (g)	Bill length (mm)	Total Head (mm)	Tarsus + toe (mm)	Wing length (mm)	Sex	Age sub	Putative species
212	27 July	139	35.2	64.6	58	180	female	adult	<i>islandica</i>
220	27 July	176	34.8	64.4	59	173	female	adult	<i>canutus</i>
230	28 July	138	35.3	67.4	57	167	female	adult	<i>canutus</i>
235	28 July	132	33.7	63.4	56	171	female	adult	<i>canutus</i>
240	29 July	138	33.4	62.0	57	172	male	adult	<i>islandica</i>
249	29 July	140	32.4	63.2	57	180	female	adult	<i>canutus</i>
259	29 July	123	34.5	65.8	57	178	female	adult	<i>canutus</i>
280	29 July	186	36.5	65.0	61	175	female	adult	<i>canutus</i>
289	29 July	141	35.2	64.2	58	173	female	adult	<i>canutus</i>
299	29 July	142	35.6	65.3	58	175	female	adult	<i>canutus</i>
302	29 July	145	35.6	67.2	58	175	female	adult	<i>canutus</i>
314	29 July	112	32.2	63.6	56	167	male	adult	<i>canutus</i>
324	29 July	130	30.9	63.6	57	157	female	2nd c.y.	<i>islandica</i>
341	29 July	141	34.1	65.0	59	177	female	adult	<i>islandica</i>

length (maximum chord) was measured to the nearest millimetre using a stopped ruler (Table 1).

We used 1.4 g radio-transmitters for the 173 MHz band width (Holohil Systems Ltd., Carp, Ontario, Canada). Individual transmitter frequencies differed by about 10 kHz. Battery-life time according to manufacturer was 42 days, and was at least 36 days in the field. Signals were listened to by using hand-held three-element Yagi antennas and portable receivers (TRX-2000S, Wildlife Materials Inc., Carbondale, Illinois, USA). The antennas were mounted at the end of long poles and positioned approximately 10 m above ground level. The signal was detected by manually turning the pole 360°. When a signal was heard, the antenna was pointed in the direction giving the strongest signal. As soon as this direction was found, background noise, amplitude of the signal as visible on the display and direction were registered. In cases where no signal was detected, only the level of background noise was noted.

We made a detailed assessment of the signal strength by varying the positions of both a receiver and a 'free' transmitter on a clear and sunny day. This test revealed strong effects on the strength of the radio signal of transmitter height, and of distance between transmitter and receiver (Table 2). Both variables together explained 52% of the variance in signal strength. The other tested variables (receiver height, the presence of an obstacle and the transmitter angle) had less, but still significant, impacts on signal strength (together they accounted for another 9% of explained variance). In practice, radiosignals could be received at maximum distance of approximately 3 km when the birds were in the air, and 1.5 km when the birds were on the ground.

**Table 2 (a).** An analysis of variance of the signal strength of the free transmitter reveals the effects of (1) the height of the transmitter, (2) the distance between receiver and transmitter, (3) the height of the receiver (4) an obstacle (a human body) just before the transmitter and (5) the angle of the transmitter antenna (tail away or perpendicular). Only distance was treated as a continuous variable, all others as categorical variables. All variables contributed significantly to the explained variance ( $p < 0.0001$ ;  $R^2 = 0.60$ ;  $n = 380$ ).

Variable	Explained variance (%)	p-value
transmitter height	29.1	<0.0001
distance (km)	22.5	<0.0001
receiver height	4.2	<0.0001
obstacle	2.3	<0.0001
transmitter angle	2.1	<0.0001

**Table 2 (b).** Parameter values for the above model.

Variable	Parameter	Effect
	constant	+0.64
transmitter height	2 m	+0.27
transmitter height	knot height	-0.03
transmitter height	on mudflat	-0.24
distance (km)	continuous variable	-0.45
receiver height	good site on bridge ship	+0.07
receiver height	hinddeck ship	+0.06
receiver height	fence on bridge ship	+0.04
receiver height	mudflat	+0.02
receiver height	bad site on bridge ship	-0.18
obstacle	no obstacle	+0.07
obstacle	obstacle	-0.07
transmitter angle	perpendicular	+0.05
transmitter angle	tail away	-0.05



From two receiving stations, one permanently based on Griend and one at variable locations on board the NIOZ-research ship RV 'Navicula', we scanned all directions for radio-signals at the appropriate frequencies in the period 27 July and 5 September 1995. The ship was mostly based at Richel, where we took readings from 27 July to 17 August, with a gap in the weekend of 4–6 August (Table 3). We also scanned Richel during high tide on 25 August during high tide. At Griend we made a continuous series of measurements from 1 August to 5 September.

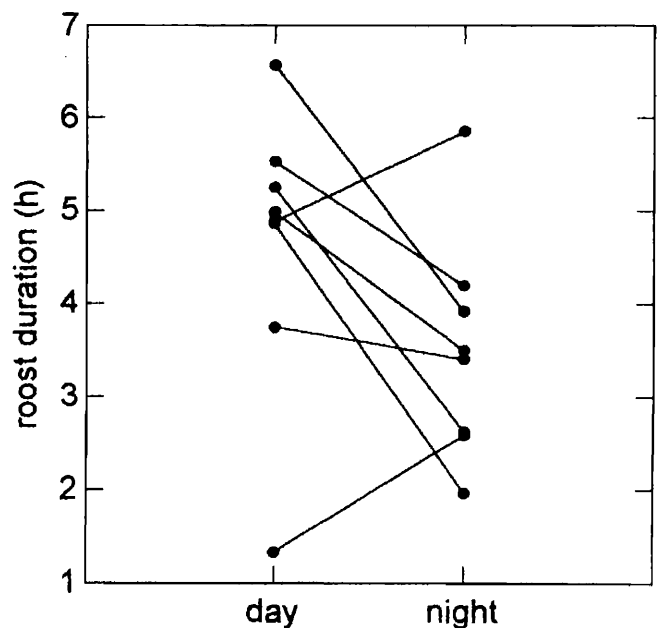
During the same period we followed flocks of feeding Red Knots at low water. We always tried to check these flocks for radiomarked birds. To ascertain their diet, droppings were collected and analysed in the laboratory according to the methods outlined by Dekinga & Piersma (1993). Benthic sampling enabled us to determine prey densities for different feeding areas. At the intertidal flats near Griend we sampled a grid of 606 stations, with grid lines 250 m apart. At each station we took one core of 1/56 m<sup>3</sup> down to a depth of 20 cm (Piersma *et al.* 1995, Piersma & Koolhaas 1997). At all other intertidal flats we sampled a total of 384 stations, which were also spaced at intervals of 250 m. In the field all bivalves, gastropods and crustaceans retained on a sieve with a 1 mm mesh were collected in plastic bags and stored frozen. Subsequently we measured lengths of the individual invertebrates to the nearest millimeter, whereafter they were incinerated at 550°C for 2 hours to determine ash-free dry mass (see Piersma *et al.* 1993a for further details of methods).

## RESULTS

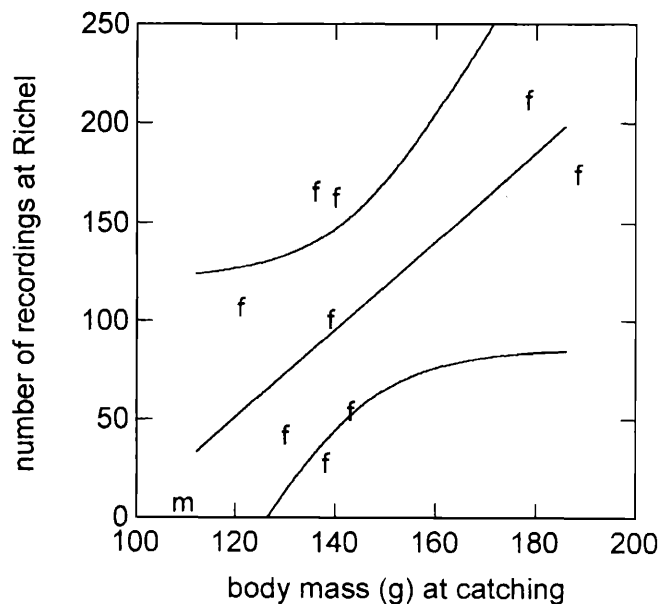
In total we made 1004 radioscans, each time checking all possible radiofrequencies. On average, an individual bird was recorded on 206 occasions (21%, SD=111 occasions). In 707 of the 1004 scans (70%) we recorded at least one radio-marked bird. On Griend the average interval between scans was 97 min (SD=155), and during periods of observation at RV 'Navicula' the interval averaged 45 min (SD=67).

We were able to obtain daily tracks of 11 individuals for about 17 days, one bird for 9 days, and two individuals for 35 days, at which point we stopped our observations. The latter two birds (#249 and #324) were the only birds recorded from 18 August onwards. All the others were absent from about that time, at least near Griend and Richel. Except for #249, the disappearance of the putative *canutus* Knots was congruent with the predicted timing of their departure from the western Wadden Sea (Piersma *et al.* 1992, 1993a).

The estimated locations of the different individual birds enabled us to derive the linear distance moved per day. For this analysis we selected cases in which we were able to track the birds from at least three different positions during a single tidal cycle. Three examples of this kind of space-use are plotted in Figure 1. In the course of a single day, birds moved



**Figure 2.** The time spent at the Richel high-tide roost was shorter during night- than during daytime highwater periods, and differs on average by 1 h 8 min (one sample t test;  $p=0.089$ ). Birds were categorized as night-time roosters when they arrived at Richel between 22:00 h and 3:00 h. The dataset includes 30 day-time observations and 10 night-time observations on 8 individuals, all of them being collected during spring tides.



**Figure 3.** Number of telemetry recordings of the 10 *canutus*-Knots in the Richel area (*i.e.* roost and nearby intertidal flats) as a function of body mass at catching (linear regression and its 95% confidence interval are shown, f=female, m=male).

on average a linear distance of 20.8 km (SD=4.6 km;  $n=15$  more or less continuous trackings). With an average of 1.97 high tides a day, this results in 10.6 km during a single tidal cycle. This estimate may be biased to the low distances, as our transmitters could never be received at distances larger than 3 km, and therefore large distances could only be measured when the research vessel also moved.



**Table 3.** Time schedule of occupation and location of both receiving stations during our study period (see Figure 1 for locations).

Period	Station 1 (RV 'Navicula')	Station 2
27 Jul – 2 Aug	Richel	no observations
2 Aug – 3 Aug (from 1 Aug)	Ballastplaat	Griend
3 Aug	Frisian coast	Griend
4 Aug – 6 Aug	no observations	Griend
7 Aug – 13 Aug	Richel	Griend
14 Aug	Posthuiswad, Vlieland	Griend
14 Aug – 15 Aug	Ballastplaat	Griend
15 Aug – 17 Aug	Posthuiswad, Vlieland	Griend
17 Aug – 5 Sep	no observations	Griend (at 25 Aug also at Richel)

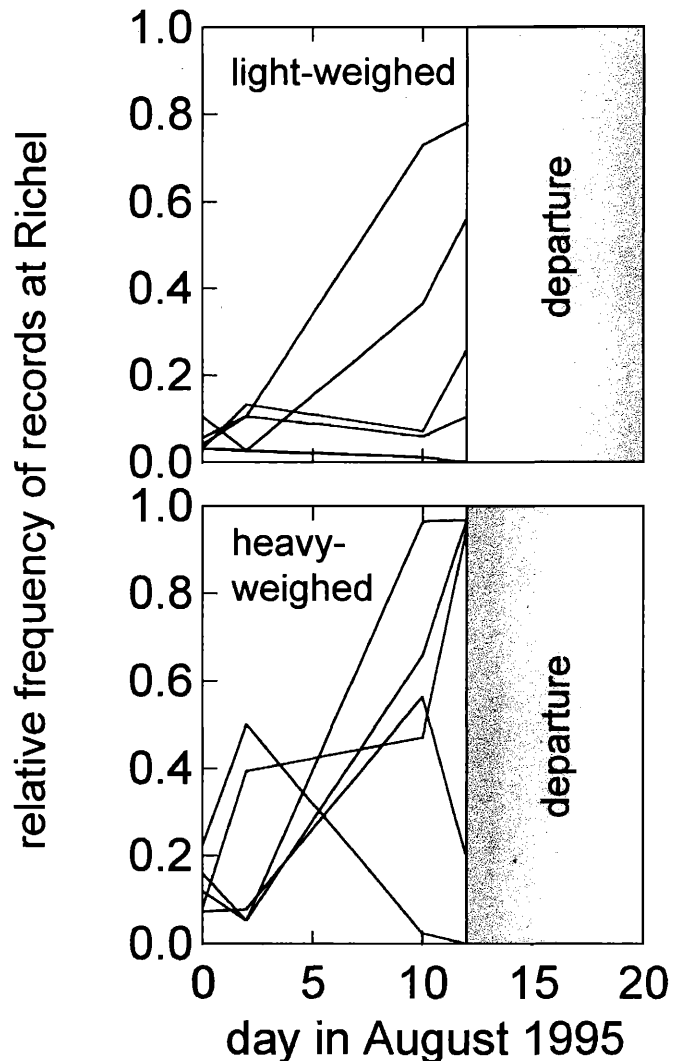
There was a tendency for Red Knots to spend shorter periods on the Richel–roost at night than during the day (Figure 2). On average, they stayed at Richel for 4 hrs and 39 min during the day, compared with 3 hrs and 30 min during the night ( $p=0.089$ ; one sample  $t$ -test).

As some of the 10 *canutus* birds not only used Richel as their high tide roost but the adjacent intertidal flats as their foraging site, it was interesting to see which individuals were so site–faithful for the entire tidal cycle. An analysis of the variation in presence at Richel, surprisingly, showed that about half of the variance could be explained by variation in body mass at marking (Table 4; Figure 3). In fact, most of the heavy individuals (body mass  $>140$  g;  $n=5$ ) steeply increased their presence in the Richel area over time, whereas for the lighter birds (body mass  $\approx 140$  g;  $n=5$ ), the presence in this area rose slower. Around 12 August, 3 of the 5 heavy individuals were almost always present at or near Richel (Figure 4).

At the intertidal flats bordering Richel high densities of juvenile shorecrabs *Carcinus maenas* were found, and this prey category indeed contributed importantly to the diet of Red Knots feeding in this area (Figure 5). Other intertidal flats were relatively poor in shorecrabs, but richer in harder–shelled bivalves such as Baltic tellins and *Macoma balthica*. When transformed into biomass values (Dekinga & Piersma 1993), the diet of birds foraging near Griend and Vlieland contained 97% molluscs, and that of birds foraging near Richel contained 51% crustaceans and only 49% molluscs.

## DISCUSSION

On the basis of observations on the movements of flocks in daytime, Piersma *et al.* (1993a) hypothesized that individual Red Knots staging in the western Wadden Sea in late summer and autumn roam over considerable distances during a tidal cycle. The present observations on radiomarked individuals confirm that hypothesis. We observed individuals that moved



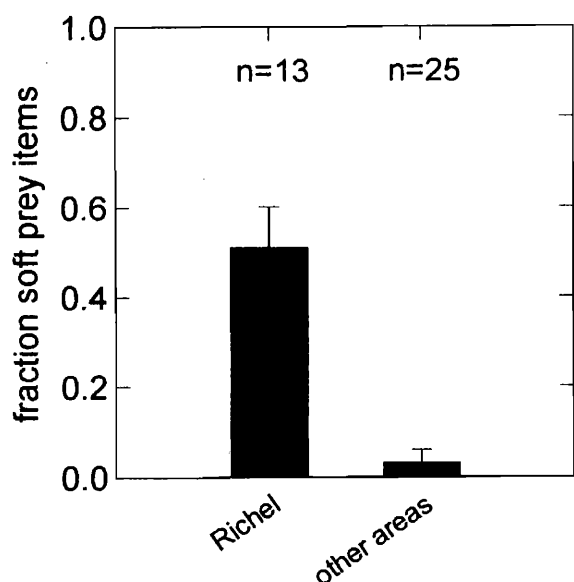
**Figure 4.** The frequency of visits of the 10 *canutus*-Knots to the Richel area increased over time. Some of the heavy-weighted individuals ( $>140$  g at catching, lower graph) reached an almost continuous presence around 12 August, a few days before their disappearance from the western Wadden Sea. The intensity of grey reflects the likelihood of departure based on literature–data.

over distances of more than 30 km per low tide period, but the average was much lower due to many birds remaining close to Richel throughout the tidal cycle.

On the coarse scale of our measurements, the use of space during the night did not differ from that during the day. This is consistent with the finding that on intertidal flats Red Knots find their prey on the basis of tactile stimuli (Piersma *et al.* 1995, 1998), and thus do not necessarily need light for prey detection. In fact, roost duration was on average roughly one hour shorter during the night than during the day, an effect that was not due to differential sampling during either spring or neap tides (all measurements were made during spring tides).

There is a whole suite of possible factors influencing the choice between different feeding areas, some of which relate to distance to the roost site (Myers 1984). For example, there





**Figure 5.** Diet composition (in terms of biomass) of Red Knots feeding near Richel, and in other areas (mainly near Griend) in early August 1995 (mean percentages and standard errors). Near Richel half of the diet consisted of relatively soft-bodied prey, mainly shorecrabs *Carcinus maenas*. The other half consisted of hard-shelled molluscs, mainly Baltic tellins and *Macoma balthica*. Almost all prey items fed upon elsewhere were of the hard-shelled kind. n indicates the number of dropping samples, each sample containing 10–300 droppings.

may be migration-related physiological changes that can play a role. Different individuals may have different needs to track changes in local food stocks and to find suitable flock-mates to take-off with. Relative risks of predation and of starvation may critically depend on body mass, as will flight costs.

If heavy individuals that are approaching their departure on a 4,000–5,000 km long flight to the wintering grounds indeed show a weight-saving strategy by reducing stomach mass (Piersma *et al.* 1993b), such birds may be forced to feed on relatively soft-shelled prey such as shorecrabs. In a year like 1995, when shorecrabs were abundant near Richel, it would thus pay off to stay there during the whole tidal cycle.

Alternatively, or additionally, recently arrived birds with lower body masses may feel a greater need to explore and cognitively map the food abundance on different intertidal areas than well-established heavy birds that are ready to go.

**Table 4.** Analysis of variance in the number of recordings of *canutus* Knots in the Richel area, as explained by body mass. In the model body mass is treated as a continuous variable. Statistics are based on 326 scans over a period of 18 days (31 July–17 Aug.) near Richel. Body mass explained significant variation ( $p < 0.03$ ).

Variables	df	SS
Body mass	1	22294
Error	8	23065
R <sup>2</sup>		0.49

At the same time remaining near the high tide roost would lead to a reduction in the daily flight costs (Piersma *et al.* 1993a), especially in heavy birds. An abundance of conspecifics may ensure that long distance-migration flights can be initiated together with sufficient numbers of like-minded conspecifics (Piersma *et al.* 1990), whether during high or during low tide. Finally, body mass dependent predation and starvation risks may influence trade-offs in the choice between roost site safety (e.g. Richel safer than Griend; Piersma *et al.* 1993a) and proximity of good feeding areas (e.g. Griend better than Richel). Future studies should clarify the importance of these different factors.

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**Appendix 1.** An overview of radio–telemetry studies on waders.

The following list is ordered chronologically. Many studies deal with habitat choice on the wintering grounds, and the differences between day and night are often stressed (e.g. Dugan 1981, Smith 1987, Summers 1994, Wood 1986). Recently, migratory routes have been explored also (Baker *et al.* 1998, Iverson *et al.* 1996, Warnock & Bishop 1996, Warnock & Bishop 1998). The larger wader species have been equipped with motion–sensitive transmitters to record activity patterns (Exo 1992, Exo 1993a, Exo 1993b).

Species	Phase of annual cycle	Research theme	Reference
Grey Plover <i>Pluvialis squatarola</i>	wintering	nocturnal feeding	Dugan (1981)
Long–billed Curlew <i>Numenius americanus</i>	chicks	movements, mortality	Redmond & Jenni (1986)
Grey Plover <i>Pluvialis squatarola</i>	wintering	diurnal and nocturnal territoriality	Wood (1986)
Green Sandpiper <i>Tringa ochropus</i>	wintering	nocturnal roosting	Smith (1987)
Wilson's Phalarope <i>Steganopus tricolor</i>	breeding	mating behaviour	Colwell and Oring (1988)
Purple Sandpiper <i>Calidris maritima</i>	breeding	incubative behaviour	Cresswell & Summers (1988)
Snowy Plover <i>Charadrius alexandrinus</i>	breeding	methods	Hill & Talent (1990)
Bristle–thighed Curlew <i>Numenius tahitiensis</i>	breeding	breeding behaviour	Gill <i>et al.</i> (1991)
Golden Plover <i>Pluvialis apricaria</i>	chicks	behaviour	Yalden (1991)
Oystercatcher <i>Haematopus ostralegus</i>	breeding	time–energy budget	Exo (1992)
Oystercatcher <i>Haematopus ostralegus</i>	wintering/breeding	foraging pattern, activity, time–energy budget	Exo (1992), Exo (1993a), Exo (1993b)
Dunlin <i>Calidris alpina</i> ;			
Western Sandpiper <i>Calidris mauri</i>	wintering/migration	methods	Warnock & Warnock (1993)
Purple Sandpiper <i>Calidris maritima</i>	wintering	diurnal and nocturnal activity	Summers (1994)
Mountain Plover <i>Charadrius montanus</i>	wintering	habitat choice, activity	Knopf & Rubert (1995)
Willet <i>Catoptrophorus semipalmatus</i> ;			
Whimbrel <i>Numenius phaeopus</i>	wintering	feeding territoriality	McNeil & Rompré (1995)
Dunlin <i>Calidris alpina</i>	wintering	habitat choice	Warnock <i>et al.</i> (1995)
Western Sandpiper <i>Calidris mauri</i>	migration	use of stopover sites	Iverson <i>et al.</i> (1996)
Golden Plover <i>Pluvialis apricaria</i>	staging	habitat choice	Ketzenberg & Exo (1996)
Willet <i>Catoptrophorus semipalmatus</i>	wintering	nocturnal habitat choice	Rompré & McNeil (1996)
Western Sandpiper <i>Calidris mauri</i>	migration	use of stopover sites	Warnock & Bishop (1996)
Western Sandpiper <i>Calidris mauri</i>	wintering	home range	Warnock & Takekawa (1996)
Red Knot <i>Calidris canutus</i>	migration	use of stopover sites	Baker <i>et al.</i> (1998)
Red Knot <i>Calidris canutus</i>	breeding	breeding biology	Tulp <i>et al.</i> (1998)
Western Sandpiper <i>Calidris mauri</i>	migration	use of stopover sites	Warnock & Bishop (1998)





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