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Source: Ardea, 97(1) : 71-79

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/078.097.0109

On 4 June 2008 Siberian Red Knots at Elbe Mouth kissed the canonical evening migration departure rule goodbye

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Leyrer J., Pruiksma S. & Piersma T. 2009. On 4 June 2008 Siberian Red Knots at Elbe Mouth kissed the canonical evening migration departure rule goodbye. Ardea 97(1): 71–79.

Observations of departing Siberian-breeding Red Knots *Calidris canutus canutus* from their central staging site during northward migration, the Schleswig-Holstein Wadden Sea, Germany, in early June 2008, challenge the established notion that departing long-distance migrating waders only leave around sunset. During four days we scanned several thousand Red Knots for colour-ringed individuals and found a total of 20 different individuals that were previously ringed at either their main wintering site, the Banc d'Arguin in Mauritania, or at stopover sites on the Atlantic coast of France. Body masses of captured Red Knots in Schleswig-Holstein were higher than 200 g and hematocrite values showed an average of 58%, clearly indicating that they were ready for take-off. On all except one evening, we noted impressive departure movements during the incoming tide. On that exceptional evening a cold front thunderstorm passed over the area. Late the next morning, thousands of Red Knots departed during the incoming tide. We assume that the birds avoided taking off in adverse weather conditions and elaborate why Red Knots presumably traded off advantages from departing during twilight. We suggest that during spring migration, schedules are so tight that further delays decrease fitness, either because it would cause another full day of exposure to high predation risk by falcons, or because of conditions upon arrival on the tundra.

Key words: *Calidris canutus canutus*, diurnal timing, long-distance flights, migration, shorebirds, twilight advantages, vocalization

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INTRODUCTION

Many otherwise diurnal bird species migrate nocturnally (Dorka 1966, Alerstam 1990, Fusani & Gwinner 2005, Bertin *et al.* 2007), departing from their stopover sites during the evening twilight period or shortly after in the first half of the night (e.g. Cochran 1987, Åkesson *et al.* 2002a, Bolshakov & Chernetsov 2004, Schmaljohann *et al.* 2007). In particular, nocturnally migrating songbirds profit from flying during the night so that they can maximize feeding time during the (most profitable) daylight period (Dierschke *et al.* 2003, Delingat *et al.* 2006), i.e. restoring energy (and water) stores, but also make use of the day to recover (Schwilch *et al.* 2002, Fuchs *et al.* 2006). Flying at night may also have energetic advantages as birds possibly minimize evaporative water loss (Klaassen 2004) and may benefit from a calmer atmospheric structure (Kerlinger & Moore 1986, Kerlinger 1995).

Yet, bird species taking off for non-stop long-distance flights that last several days, notably waders (or shorebirds), have always been observed to also depart from their stopover sites exclusively during the hours around sunset (Blomert *et al.* 1990, Piersma *et al.* 1990a,b, 1991). Even though the motivation for such a timing of departure at dusk is not as obvious for waders as it is for songbirds, Piersma *et al.* (1990b) provide several reasons why evening departures would still be

the most appropriate. Besides energetic and meteorological reasons, orientation issues may be important. To navigate their flight, migratory birds use several compass systems derived from the geomagnetic field, the stars, the sun and polarized skylight patterns (e.g. Åkesson & Hedenström 2007). These compass systems have to be calibrated, and birds may either calibrate their magnetic and other compasses with the help of polarized skylight patterns vertically intersecting the horizon at sunrise and sunset (Cochran *et al.* 2004, Muheim *et al.* 2006, 2007) or, conversely, may adjust their celestial compass by means of magnetic cues (e.g. Wiltschko *et al.* 1998a, 1998b). Either way, all studies suggest that the twilight period might be a critical time of the day for birds to get their bearings.

Before birds can take off, they need to fill up the energy stores to fuel their flights. Embarking on non-stop flights of several thousand km, Red Knots *Calidris canutus* have usually nearly doubled body mass (Piersma *et al.* 2005). The daily routines of Red Knots and other obligate users of intertidal areas are governed by tides rather than a circadian rhythm (van Gils & Piersma 1999, van Gils *et al.* 2006). Still, if foraging is more profitable during daylight than at night, waders would maximize fuelling by leaving for their long-distance flights with the rising tides in the evening (Lank 1989).

Observations of departures of Siberian-breeding Red Knots *Calidris canutus canutus* from their central staging site during northward migration, the Schleswig-Holstein Wadden Sea, Germany (see Prokosch 1988, Piersma *et al.* 1992, Fig.1), in early June 2008, challenge the established notion that departing long-distance migrating waders only leave around sunset. Here we provide a full description and interpretation of our observations on the assembly and flight behaviour of these Arctic-breeding waders with one of the latest seasonal migration schedules published (Piersma *et al.* 1990a).

STUDY SITE AND METHODS

Between the evening of 31 May 2008 (from around 9:00 pm) until the afternoon of 5 June 2008 (around 2:00 pm) we observed wader stopover behaviour during northward migration at the mudflats of Nordergründe, Dithmarschen, at the north-eastern shores of the Elbe river estuary in the German Wadden Sea (53°55.96'N, 08°52.13'E, Fig. 1). Observations were made continuously from the mudflats and from aboard the research vessel *Navicula*. In the course of the observation period evening high tides shifted from 10:22 pm (31 May) to 2:14 am (5 June) (high tides for Büsum, BSH 2007). Observations were made using telescopes (80x magnification) and/or binoculars (10x40 magnification). Whilst observing departing Red Knots, their departure calls were recorded on the mudflats. Records were digitally cleaned and images were produced using RavenLite 1.0 Build 9 Update 10, by Cornell Lab of Ornithology Bioacoustics Research Program.

Intensive catching and colour-ringing of Red Knots in their main wintering areas in previous seasons (Dutch Wadden Sea, French Atlantic Coast, Banc d'Arguin, Mauritania; Piersma & Spaans 2004) enabled us to identify individuals and subspecies identity. When a flock of Red Knots was encountered, we checked for colour-ringed individuals.

Between 2 and 5 June 2008 we caught Red Knots during the night high tides on the mudflats close to our research vessel using mist nets. Birds were ringed with a German metal ring ("Vogelwarte Helgoland") and a unique colour-ring combination. The Red Knots were measured (Prater *et al.* 1977) and weighed to the nearest g using an electronic balance. Breeding plumage was scored on a scale from 1 to 7, with 1 being full winter and 7 being full breeding plumage (Piersma & Jukema 1993). A blood sample was taken from the wing vein to measure hematocrite (Hct) values as a measure of migratory readiness (see Landys-Ciannelli *et al.* 2002) as well as for subsequent molecular sexing (Baker *et al.* 1999). For Hct measures, 25 μl were filled into heparinized micro-hematocrite capillary tubes. The tubes were centrifuged at 10 000x g for 10 min. After centrifugation, Hct (packed red cell volume) in the capillary tubes was measured with a ruler as the percent cellular fraction of total blood volume (see also Landys-Ciannelli *et al.* 2002). Blood samples were taken with permission from the Ministerium für Landwirtschaft und Umwelt, Kiel, Germany.

RESULTS

Observing departing migrants

In the evenings of 1 and 2 June we observed departing flocks during the times of twilight and incoming tides. We identified departure behaviour as a combination of the following indicators: Red Knots were very communicative during the low tide period (also singing and displaying individuals, see Piersma *et al.* 1991 and Swennen 1992) and many of the birds were roosting at a time when they should have been foraging (Swennen 1992). Towards the end of the low tide period, when the incoming tide was flooding the mudflats and the birds usually would have been forced to fly to their high

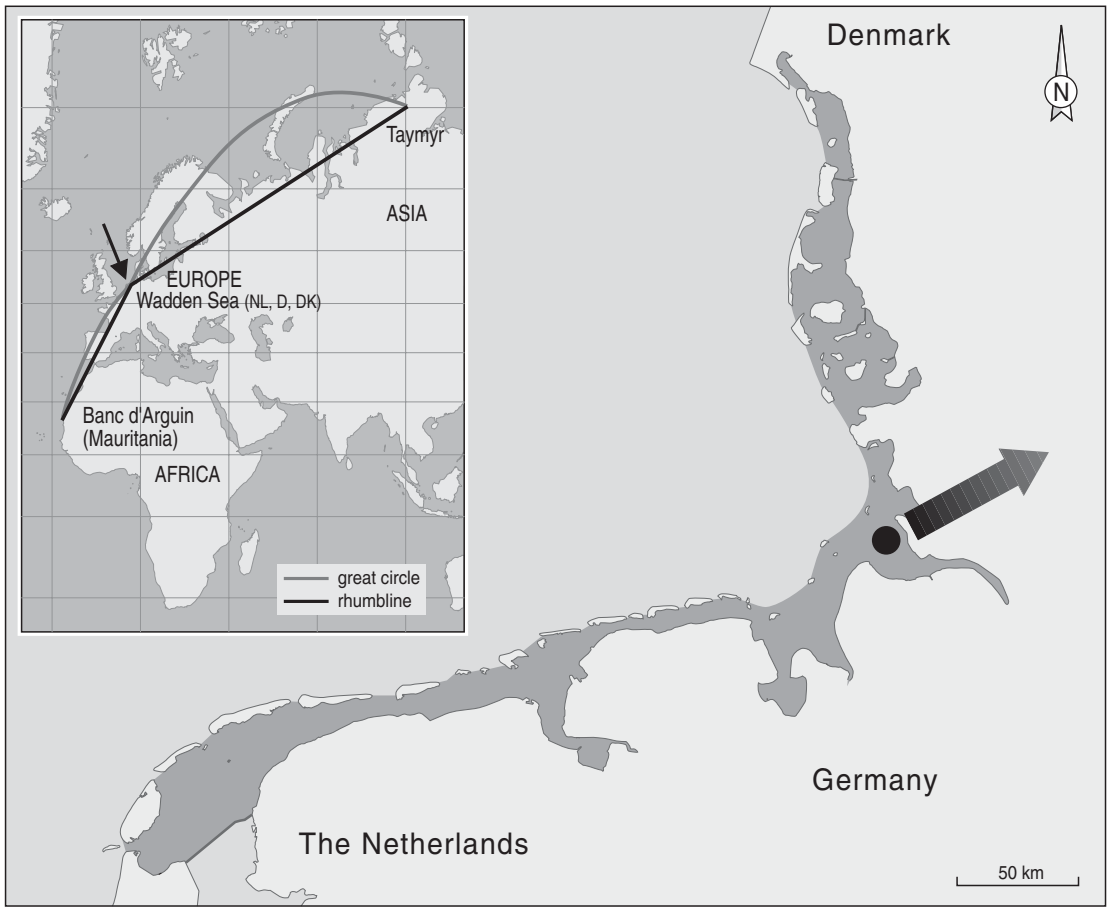

Figure 1. The eastern part of the Dutch-German-Danish Wadden Sea (dark grey shaded area) represents the central stopover area for northward migrating Afro-Siberian Red Knots. The black dot locates the Nordergründe mudflats, Dithmarschen, Schleswig-Holstein, Germany, north of the Elbe river estuary. The arrow indicates the general flight direction (about 70°, ENE) of departing Red Knot flocks on their way to their breeding area, the Taimyr Peninsula, Siberia, presumably following the rhumbline route. The inset shows two possible routes Red Knots may follow from their Mauritanian wintering grounds to the Siberian breeding grounds: the great circle route and the rhumbline route. The arrow is indicating the study area.

tide roosts, flying flocks of several tens to hundreds of individuals gained height whilst forming the typical formations of migratory flights (Piersma *et al.* 1990b) and vocalizing typical 'veek' calls (Fig. 2). The birds eventually disappeared out of sight into north-easterly directions (the direction of Siberia). On 1 June we observed two flocks of 250 and 120 Red Knots departing in an ENE direction around 9:00 pm and 9:20 pm, respectively. The latter flock was joined by 10 Ringed Plovers *Charadrius hiaticula*. On the following evening (2 June) we again observed two departing flocks of 25 and 240 Red Knots leaving into an ENE direction at 8:33 pm and 9:00 pm. By means of binoculars, flocks usually could be followed for 2–5 min, depending on the overall visibility.

A low-pressure front system bringing along a huge thunderstorm with heavy rains coming from SW crossed the southeastern shore of the North Sea (the Wadden Sea coast of Lower Saxony and southern Schleswig-Holstein, Germany) on the early evening of 3 June (Fig. 3). Around 7:00 pm it hit the coast of Dithmarschen and the adjacent mudflats of Nordergründe. Heavy rainfalls as well as gusty winds from SW were dominating the main part of the twilight/incoming tide period, and no departing flocks were observed, although during the preceding daylight low tide period we observed the same pre-departure behaviour as on the days before. The thunderstorm lasted for about 3 hours, followed by the odd rain shower and drizzly but calmer weather. The next morning the weather was dry

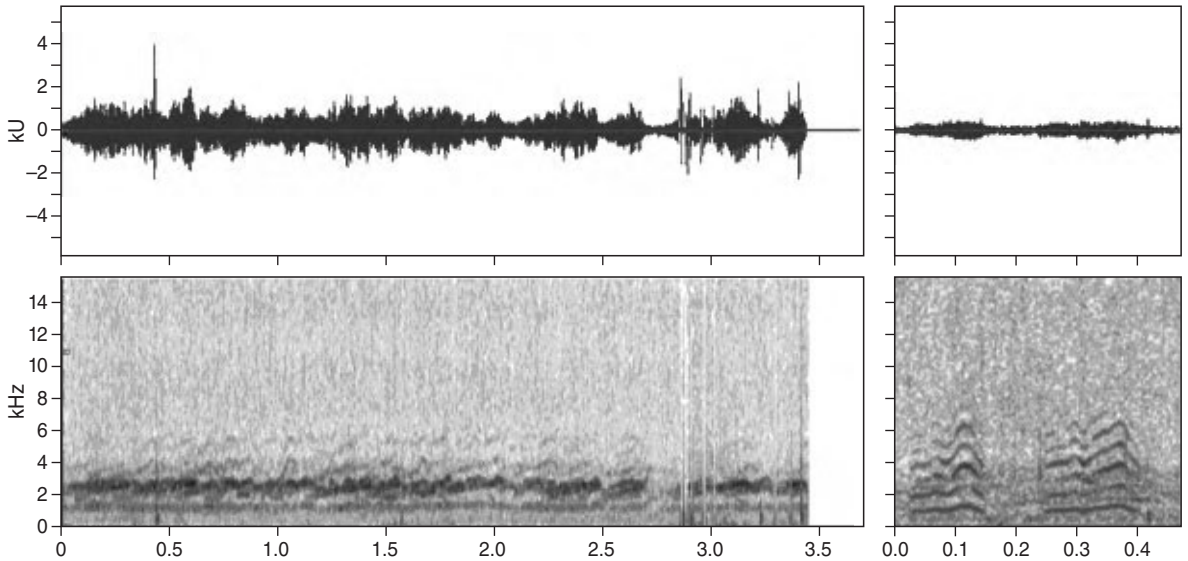

Figure 2. Waveform and spectrogram of departure calls of a Red Knot flock of 160 individuals departing from Nordergründe on 2 June 2008 at 9:05 pm in an east-north-easterly direction. Left panel shows calls of several Red Knots in a flock, right panel shows two single calls of a Red Knot departing separate and c. 10 s after the main flock.

and calm again and during that low water/incoming tide period we were surprised to observe massive departure movements of waders, especially Red Knots. Between 11:00 and 12:00 we observed 10 000s of Red Knots, but also Ringed Plovers, and, to a lesser extent, Dunlins *Calidris alpina* leaving the mudflats in flocks of 100–200 individuals in NNE directions, departing for their Siberian breeding grounds, identifiable again by calls and the shape of their formations (Piersma *et al.* 1990b, 1991).

The meteorological context of this event

During the second half of May 2008 and the first days in June 2008 wind was generally blowing from easterly directions. Wind was calmest during the early evening of 1 June 2008 when speeds averaged at 2 m/s (2 Beaufort, Bft) from a SE direction (wind speed and direction recalculated using the NCEP database (http://www.cdc.noaa.gov/), calculated for sea level). All other three following evenings (2–4 June 2008) wind speed was approximately 5–6 m/s (4 Bft) and direction changed to NE on 2 and 4 June, while on 3 June winds blew in general from a SE direction. In the course of the night, wind speed tended to generally increase by 1 Bft, except for 2 June when wind decreased by 1 Bft. Except for 1 June wind also slightly changed direction during the night, but in general keeping an easterly direction: 1 June SE 3 Bft, 2 June SE 3 Bft, 3 June E 4 Bft, 4 June E 4 Bft.

Satellite images from the NERC Dundee Satellite Receiving Station (http://www.sat.dundee.ac.uk/) provide a retrospective about cloud coverage during the first days of June 2008. On the evening of 1 June no clouds were to be seen from the Wadden Sea across the Baltic Sea up to Finland (the potential flight route, see inset Fig. 1). The evening of 2 June shows some rather spotty and thin cloud cover over the Wadden Sea, but still no clouds across the Baltic Sea as far as the White Sea. The evening of 3 June is documented in Fig. 3, with a large band of thick clouds over the Wadden Sea area, but no clouds further northeast over Scandinavia and the Baltic Sea. The satellite image of the very early morning of 4 June still shows a band of clouds over the Wadden Sea which became thinner in the course of that morning until midday. The sky was nearly 100% overcast when we were observing our departing Knots on 4 June around midday, but the clouds were a thin layer of high fog rather than rain clouds.

The provenance of the birds

In the evening of 1 June 2008 we scanned about 3800 Red Knots for colour-ringed individuals and found three Red Knots that had been previously ringed on the wintering grounds of the Afro-Siberian Red Knot on the Banc d'Arguin, Mauritania. On the following morning (2 June 2008) we checked around 3000 Red Knots and found a total of 13 colour-ringed individuals (all different from the day before). Twelve Red Knots were

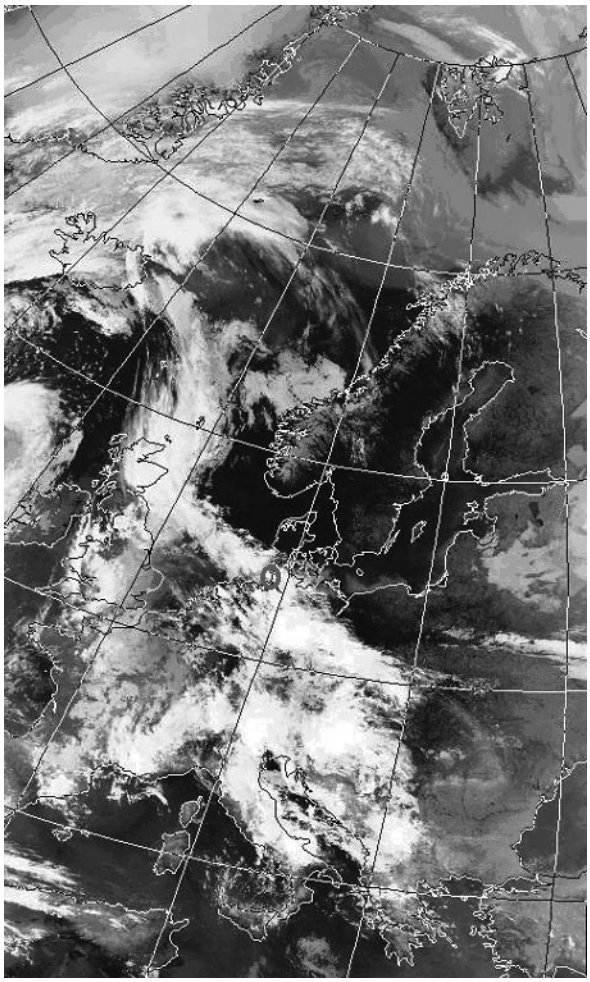

Figure 3. Satellite image of the low pressure system passing the Southern North Sea coast on the evening of 3 June 2008. The study area is marked with a circle. The image was made by satellite NOAA-17 at 8:28 pm and shows AVHRR channel 4. Advanced Very High Resolution Radiometer (AVHRR) instruments measure the reflectance of the earth in various band width; channel 4 is sampling in the infrared window and is primarily used for measuring sea surface temperatures and day and night cloud mapping. The image has been downloaded from the NERC Satellite Receiving Station, Dundee University, Scotland (http://www.sat.dundee.ac.uk/).

ringed in their wintering grounds on the Banc d'Arguin, one individual was ringed at the Vendée, French Atlantic coast, at a time when the Afro-Siberian population of the Red Knots is stopping over at this site (Dick *et al.* 1987). This French Red Knot had been sighted exactly one year before only a few km further north (at Meldorfer Bucht, Dithmarschen on 2 June 2007). On 3 June 2008 about 1000 Red Knots were checked for colour-ringed individuals, and again two Red Knots ringed on the Banc d'Arguin as well as one Red Knot ringed at the French Atlantic coast and one individual previously ringed on Texel, The Netherlands, were found. None of these had been seen the days before. The Mauritanian and the French birds belonged to the Afro-Siberian population. The Red Knot ringed on Texel probably belonged to the Nearctic population *C. c. islandica* which is supposed to have left the area already by begin/mid May (Prokosch 1988, Davidson & Wilson 1992). After the departure event, on 4 and 5 June 2008, only very low numbers of Red Knots remained foraging or roosting on the surrounding mudflats. About 60 Red Knots could be checked for rings but none were found.

The migratory state of the Red Knots

In total, we captured 13 adult Red Knots. Eleven individuals were in breeding plumage showing plumage scores of 5 and higher. Only two individuals had plumage scores of 3 and 4, i.e. they were moulted only about half way through into breeding plumage. The birds had an average body mass of 204 g (SD 21 g, range 156–227 g). Hct values averaged at 58% (range 54–67%).

DISCUSSION

Red Knots that were about to depart for (onward) migration expressed their typical intense vocalizations (Piersma *et al.* 1990b), and we show here that these mostly consist of 'veek-veek' calls (Fig. 2). 'Veek-veek' calls were heard especially when the birds started to gain height, quite a different context from their described use as 'alarm calls' of anxious birds (Cramp & Simmons 1983, BWPi 2004). In aviaries, these calls can indeed be heard after human disturbances, but also frequently during May and June (pers. obs.).

For the Afro-Siberian Red Knot, the southern areas of the Schleswig-Holstein Wadden Sea present the gateway for the last leg of their northward migration (Dick *et al.* 1987, Prokosch 1988, Piersma *et al.* 1992, Piersma *et al.* 1994). Red Knots setting off from this central staging site by the end of May/beginning of June, presumably fly c. 5000 km non-stop directly to their Siberian breeding grounds on the Taimyr peninsula (Dick *et al.* 1987, Piersma *et al.* 1992). With body mass values higher than 200 g, the Knots we observed would have had enough energy stores to cover the last leg of their northward migration (Prokosch 1988, Piersma *et al.* 1992). Landys-Ciannelli *et al.* (2002) showed that in Bar-tailed Godwits *Limosa lapponica*,

hematocrite values of more than 50% clearly indicated migratory readiness. Wintering Knots on the Banc d'Arguin, Mauritania, in December usually show hematocrite values well below 50% (J. Leyrer *et al.* unpubl. data). Hence, the high body weight and the high (>54%) hematocrite values make us feel confident in assuming that we indeed observed Afro-Siberian *canutus* Knots leaving for their Siberian breeding ground.

Recent population estimates of the Afro-Siberian Red Knots state the population size at approximately 400 000 individuals (Wetlands International 2006, B. Spaans, pers. comm.). Subtracting first-year birds that are supposed to spend their first summer in their wintering areas, roughly 250–300 000 individuals should use the Schleswig-Holstein Wadden Sea as a stopover site during northward migration. With 10 000s of individuals taking off during midday of 4 June, we observed approximately 5–10% of the whole population departing for their breeding grounds in a very narrow time window of only a few hours.

Departures of Afro-Siberian Red Knots from the Wadden Sea are usually observed in the evenings during the incoming tide in the first days of June (own obs.). At Lund, southern Sweden, a site that Red Knots pass over after leaving the Wadden Sea, radar observations have repeatedly shown peak passage by 5–6 June (Gudmundsson 1994), with arrivals on the Siberian tundra regularly around 10 June (P.S. Tomkovich, pers. comm.). These observations suggest a rather predictable seasonal schedule. Yet, it is still unclear what exactly triggers the rather predictable evening departure time.

Birds that soar and glide, e.g. storks and eagles, almost always migrate during daytime because they depend on thermals that only exist when the sun is heating the earth (Shamoun-Baranes *et al.* 2003a,b). Powered fliers, i.e. birds that use flapping flight, tend to migrate during the night. The larger species amongst them, like geese, ducks, gulls, terns and waders cover the distances between wintering and breeding grounds in several thousand km long non-stop flights (Piersma 1987, Alerstam & Gudmundsson 1999, van de Kam *et al.* 2004, Schmaljohann *et al.* 2008), flying both day and night. Nevertheless, descriptions of departure behaviour consistently report that wader flocks embarking on long-distance flights do so before or just after sunset, even in species that experience a tidal rather than a diurnal rhythm (Lank 1989, Blomert *et al.* 1990, Piersma *et al.* 1990a,b, 1991, Swennen 1992).

Birds taking off for migration seem to benefit greatly from spending the twilight period prior to departure calibrating their compass systems (Wiltschko *et al.* 1998a,b, Åkesson *et al.* 2002b, Cochran *et al.* 2004, Muheim *et al.* 2006, 2007). Yet, Cochran *et al.* (2004) suggest that a calibration of the magnetic compass by means of polarized light could be accurate for several days because solar twilight azimuths change only slowly with time and thus birds could be guided by a previously calibrated compass. Since Red Knots stay in the area for up to three weeks for refuelling their energy reserves, it is not impossible that our Red Knots have calibrated their navigational systems already previously. We just do not know whether birds constantly update their compasses in order to be able to navigate their long-distance flights, or if this belongs to any last minute preparations just prior to the actual onward flight. If calibrating any compass against other cues shortly before departure provides navigational advantages, these advantages were traded off by our observed midday-departing Red Knots for something that is yet unknown.

At the latitudes of the Wadden Sea in early June nights are short. Thus, evening rather than morning or midday departures should not make a huge difference in terms of avoiding heat stress by flying at night. Furthermore, flying will be mostly in daylight conditions as most of the route is north of the Arctic Circle with no real darkness at all during that period of the year. In the Wadden Sea, Red Knots have a tidal rather than a diurnal rhythm. Still, scheduling the departure for long-distance flights explicitly for the evening incoming tides is supposed to be the rule rather than the exception. If foraging by daylight is more profitable than during the night, Red Knots could gain a few extra hours of foraging time by leaving with the evening tide. However, during the low tide period before evening departures, large groups of Red Knots were roosting and preening. This has also been observed in *islandica* Knots before departing from the Wadden Sea for their subsequent (final) stopover site on Iceland (Swennen 1992). Having filled up their energy stores, the Red Knots obviously were ready for take-off and this includes, besides having built up flight muscles, having reduced the size of their digestive system (Piersma & Gill 1998, Piersma *et al.* 1999).

Embarking on a non-stop flight of several thousands of kilometres and for several days with a limited energy load, birds should make use of favourable winds (see e.g. Liechti 2006) and thus avoid taking off with adverse weather conditions like those on the evening of 3 June. Over the previous days, wind conditions had been rather stable with constant but light to moderate winds coming from an easterly direction as well as dry weather. In terms of wind and rain, Red Knots taking off on 4 June midday experienced weather that had not

changed since the passage of the thunderstorm the evening before. Still, they departed late the next morning, rather than taking off during the morning twilight period or waiting another ten hours for the following sunset period.

Departures at 'odd' times have been reported for Schleswig-Holstein before (Piersma *et al.* 1991). Taking off in early June, *canutus* Knots are the latest waders to leave for the Arctic breeding grounds (Prokosch 1988, Piersma *et al.* 1990a) and the latest subspecies that moves north (Piersma *et al.* 2005). It is very likely that the birds are on a tight schedule in order to arrive at their breeding grounds at the optimal date (e.g. Drent *et al.* 2003). According to migration theory, migratory birds are either time or energy selected, or they try to minimize the predation associated mortality risk (Alerstam & Lindström 1990). Several studies have described the influence of predation risk on the migratory performance (e.g. Lindström 1990, Ydenberg *et al.* 2002, Nebel & Ydenberg 2005), and recently, focus has been set especially on the interplay between wader migration and Peregrines *Falco peregrinus* in particular (Ydenberg *et al.* 2004, 2008, van den Hout *et al.* 2008). In the Wadden Sea, Peregrines may have adjusted their breeding schedule according to the migratory schedules of waders by starting incubation about one month later than their conspecifics further inland (Robitzky 2002, P.J. van den Hout, pers. comm.). In this respect, we suggest that the need to reduce predation risk might have triggered the 'odd time departure event'. Red Knots that are ready to go have reduced flight manoeuvrability (Dietz *et al.* 2007) and thus have extra reasons to avoid the attentions of falcons and other raptors. Close to our study area, on the island of Trischen, at a distance of about 20 km, a pair of Peregrines was breeding and several Red Knot carcasses have been found near the nest, amongst them a French-ringed *canutus* Knot (M. Dorsch, pers. comm.). Perhaps, by leaving in the morning after an evening when the weather prevented departures, the birds simply avoided another day of exposure to falcon predation.

ACKNOWLEDGEMENTS

We thank Tony van der Vis and Hein de Vries on board RV *Navicula* for being such excellent crew, Anne Dekinga, Sarah Engelhard, Anne Schrimpf and Mirjam Szwierczynski for good company and all kinds of help. We also thank Judy Shamoun-Baranes for making the satellite images available to us. We are very grateful to Judy Shamoun-Baranes, Heiko Schmaljohann, and Rachel Muheim for very valuable comments on an earlier version of the manuscript and to Harry Zwerver for his help with 'cleaning' the sound recordings of the departing Knots. The Nationalparkamt Tönning kindly gave permission to work within the Nationalpark 'Schleswig-Holsteinisches Wattenmeer'. Financial support came from MAVA Foundation for Nature Conservation, Switzerland. .

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SAMENVATTING

De meeste trekvogels zitten krap in hun tijd. Dat geldt zeker voor de Afro-Siberische ondersoort van de Kanoet *Calidris canutus canutus*. Deze Kanoeten overwinteren vooral op de Banc d'Arguin in Mauritanië. Begin mei vliegen de meeste non-stop naar de Duitse Waddenzee in Sleeswijk-Holstein, een afstand van bijna 5000 km. Daar hebben zij slechts drie weken de tijd om genoeg lichaamsreserves aan te leggen voor een vlucht naar hun broedgebieden op het schiereiland Taimyr in Siberië, nog eens een non-stop vlucht van 5000 km. Voor Kanoeten is het cruciaal om daar op tijd aan te komen, maar onderweg beïnvloeden weersomstandigheden hun mogelijkheden. Verder is oriëntatie een belangrijke factor voor trekvogels. Zij navigeren met behulp van verschillende kompassystemen (aardmagnetische veld, zon en sterren). Deze systemen moeten nu en dan met elkaar worden gelijkgesteld. Dit kalibreren lukt het best rond zonsondergang (en zonsopkomst), als alle 'cues' zowat tegelijkertijd aanwezig zijn. Misschien vertrekken veel trekvogels daarom rond deze tijd. Van Kanoeten is bekend dat ze juist in de vroege avond, voor zonsondergang, liefst met opkomend water vertrekken. 's Nachts vliegen geeft als extra voordelen de lagere temperaturen (vliegende vogels moeten warmte kwijt) en een rustiger atmosfeer dan overdag. De *canutus* Kanoeten vertrekken begin juni vanuit hun opvetgebieden in de Waddenzee van Sleeswijk-Holstein. Na enkele dagen met vertrek op normale tijdstippen, observeerden wij op 4 juni 2008 tienduizenden Kanoeten die niet rond zonsondergang, maar tijdens opkomend water midden op de dag vertrokken. De avond ervoor was er onweer in het gebied. Het was toen te slecht om te vertrekken. Toch hebben de vele Kanoeten (misschien wel 5–10% van de hele trekkende populatie) de volgende avond niet afgewacht. Wij suggereren dat zij met het middagvertrek de voordelen van een avondstart hebben ingeruild voor een ander voordeel. Omdat in de buurt Slechtvalken *Falco peregrinus* broeden, die in deze tijd veel steltlopers vangen, is het mogelijk dat ze een hele extra dag met een verhoogd predatierisico (ze zijn immers heel vet en minder wendbaar) niet hebben willen afwachten.

Corresponding editor: Dik Heg
Received 26 August 2008; accepted 3 December 2008

ARDEA

TIJDSCHRIFT DER NEDERLANDSE ORNITHOLOGISCHE UNIE (NOU)

ARDEA is the scientific journal of the Netherlands Ornithologists' Union (NOU), published bi-annually in spring and autumn. Next to the regular issues, special issues are produced frequently. The NOU was founded in 1901 as a non-profit ornithological society, composed of persons interested in field ornithology, ecology and biology of birds. All members of the NOU receive *ARDEA* and *LIMOSA* and are invited to attend scientific meetings held two or three times per year.

Layout by Dick Visser, Haren, The Netherlands
Printed by Van Denderen, Groningen, The Netherlands, April 2009